PHYTOGEOGRAPHIC STUDIES IN THE ATHABASKA–GREAT SLAVE LAKE REGION, II

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With five plates and six text-figures

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ABSTRACT

THE FORESTS of the Athabaska–Great Slave Lake region are described in seven types (pp. 37–61). The first three are composed principally of white spruce, *Picea glauca* s. 1., but differ in composition, structure, history, and geographic position. The remaining four are of jack pine, balsam fir and white spruce, black spruce and lodgepole pine, and bog forest of black spruce. Park-like white spruce forests have their greatest development near the arctic timber line, on some of the most youthful land surfaces which the region affords — surfaces exposed at the retreat of the last glacial ice from the lake region and at the drainage of the last glacial lakes. Flood plain white spruce timber is concentrated principally on the great flood plains and deltas of the Athabaska, Peace, and Slave Rivers, also on very young surfaces. Upland mesophytic forests of white spruce are mainly on deposits of glacial till and outwash that overlie rocks of Paleozoic or Cretaceous age. Nearly all of them are on surfaces exposed at earlier stages of ice and lake withdrawal (pp. 24–30). These surfaces are, in general, progressively older from northeast to southwest. Jack pine forests are most extensively developed over the pre-Cambrian rocks of the Laurentian Plateau. They are bounded on the northeast by the park-like white spruce type and on the southwest by flood plain and upland mesophytic white spruce forests. In this region the pine is regarded as a primary type, but in the upland mesophytic spruce it also occurs extensively as a fire tree, along with trembling aspen and balsam poplar. Forests of balsam fir and white spruce are confined to the flood plain of the Athabaska and Clearwater Rivers, in the southern part of the region. Black spruce–lodgepole pine timber has been found thus far only on the Caribou Mt. Plateau north of the lower Peace River. Bog forests of black spruce and larch are widespread in the region, with no obvious relation to age of surface, but with some concentration on the Laurentian Plateau where undrained, bog-filled depressions are extremely numerous (pp. 61–64).

Floristically the region is a part of the meeting-ground of northern Rocky Mountain and eastern Canadian forest elements (pp. 72–74). It is presumed that the late Wisconsin (W_3) ice advance destroyed the interglacial connections between these eastern and western elements, and that the relics thus isolated are still in process of being rejoined. The least mesophytic species in the region — the spruces, white birches, larches, and aspens — probably were least restricted by peri-glacial conditions and have been the most successful at merging their relic populations. The most mesophytic species, the balsam firs, have been least successful, and apparently have not yet overlapped the ranges of their eastern and western

components. The pines and probably the balsam poplars appear to be intermediate between the above categories (pp. 74–75). Eastern and western elements are still taxonomically distinct among the firs and pines, but among the species complexes in which merging has occurred only varietal distinctions are possible, with an abundance of intermediate forms.

The advance of forests into the Athabaska–Great Slave Lake region is thought to have been conditioned by the progressive amelioration of climates, by the progressive availability of land surfaces and suitable soils, and by the availability of tree populations from which the immigrants could come (pp. 72–73). The order of appearance of these immigrants was in turn conditioned by their general position in the Canadian forests with regard to subarctic climatic zones (pp. 64–72), and by the extent to which their migratory capacities were altered by the vicissitudes of the late Wisconsin glacial period (p. 74).

The earliest forests are thought to have been of white spruce from the foothills of the northern Rocky Mountain region, and to have entered the lake country from the southwest and west. The eastern elements are presumed to have come later, the jack pines occupying the sterile soils of the Laurentian Plateau, and the eastern white spruces interbreeding with the western forms (var. *albertiana*) on the Alberta Plateau and the river lowlands. The park-like white spruce type is thought to be a relic of the early western population, more or less isolated by the jack pine belt which has been preserved and accentuated by the sterility of the Laurentian area (p. 75).

Evidence is presented which indicates that there were no forests of large extent in central or southern Alberta or in Saskatchewan during late Wisconsin time, and that they did not appear in the southern part of the Mackenzie basin until after the final disappearance of the ice from Great Slave Lake and the drainage of the 800-foot post-glacial lake (pp. 75–78). It is thought that these events may have occurred as late as 7000–9000 years ago, bringing the advent of forests to the Athabaska–Great Slave Lake region into the period of the widely postulated post-glacial climatic optimum (pp. 69–71).

INTRODUCTION

AN ANNOTATED catalogue of the vascular flora of the Athabaska–Great Slave Lake region was published in 1936 as Part I of a phytogeographic study of that district. It was intended that Part I should be followed by another paper which would describe vegetational features; and the whole was to be a companion piece to two of my earlier papers on the plant life of the central and southern portions of the Mackenzie drainage basin (1934, 1935.) Preoccupation with other projects has delayed the completion of the proposed Part II, although sections of it have been written at intervals during the past nine years. Recent interest in our northwestern subarctic engendered by the war suggests the advisability of presenting such of this material as has been prepared. It will be published, therefore, not as a single "Part II," but as a series of parts dealing with the various kinds of plant communities. The present paper will have to do first with an outline of the botanical exploration of the region, some notes on its geological history, a general outline of its types of vegetation, and a discussion of its forests. Part III will be devoted to pond and pond-shore communities, and Part IV to the shore vegetation of the larger lakes. Other parts will deal with the vegetation of sand dunes and the lichen-heath communities of sand plains and rock outcrops.

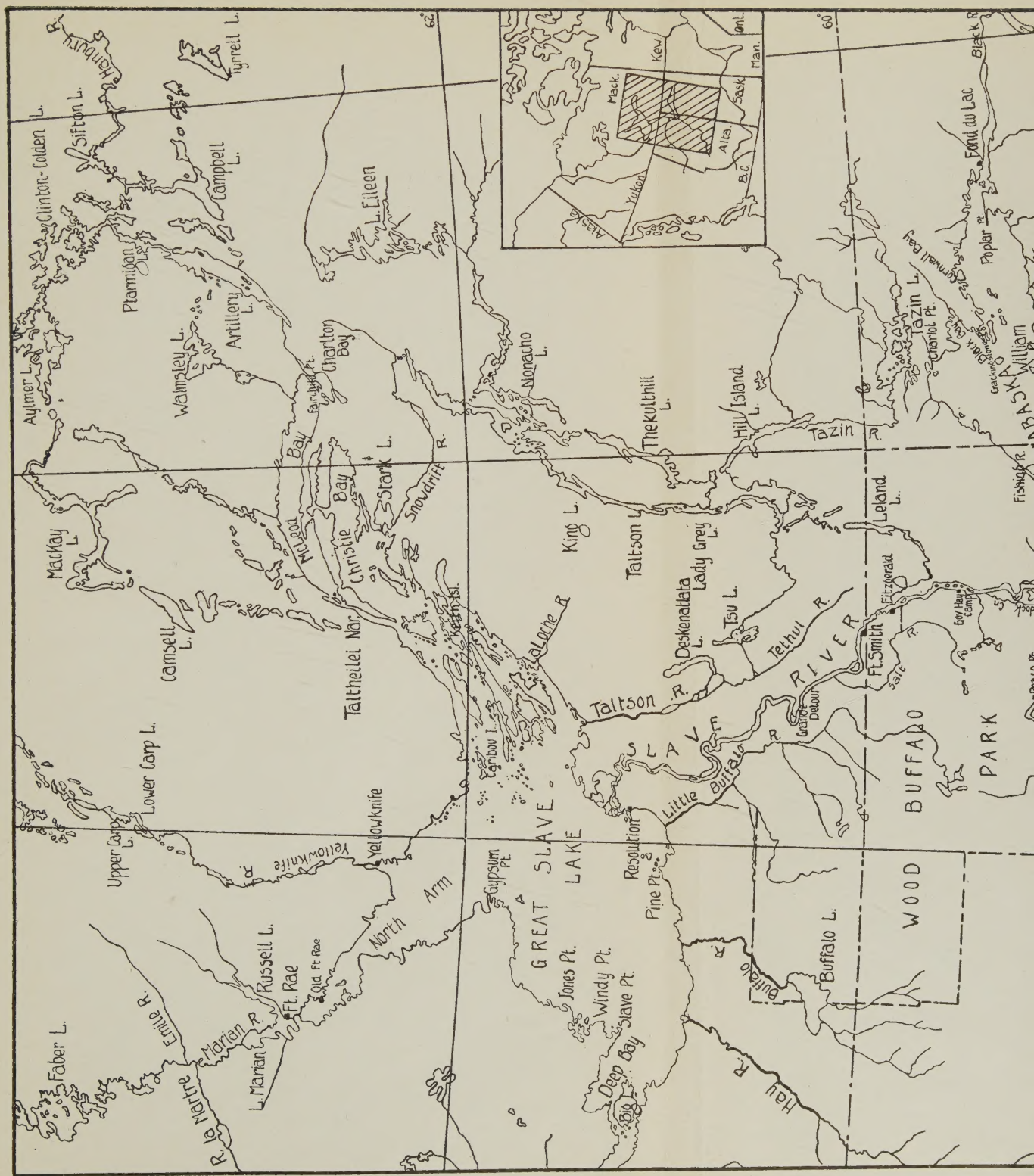I have already discussed briefly in earlier papers certain aspects of the

vegetation of the Athabaska–Great Slave Lake region. The first of these (1928) were in the form of thesis abstracts dealing with the Shelter Point area on the north shore of Lake Athabaska, and with the Fort Reliance sand plain at the eastern end of Great Slave Lake. The latter paper was subsequently published in expanded form (1930). A brief but somewhat generalized discussion of the distribution and affinities of the vegetation of the whole area was published at about the same time (1930), and some phases of the identity and distribution of forest types were described in a short paper on the white spruce and Banksian pine in northwestern Canada (1933). Suggestions and conclusions set forth in these papers, altered or expanded in the light of later studies, will be summarized here. The greatest amount of overlap, however, will be found between the present and subsequent papers and that treating the vegetation of the Wood Buffalo Park (1935). The Park area is in reality a part of the great lake region of the Mackenzie basin, and although some phases of its plant cover, such as its grasslands, are more or less unique, and although one of the principal floristic boundaries in the region as a whole is approximately at its eastern border, it is difficult to outline the plant geography of the entire area without involving it. Much of my earlier discussion of its vegetational features will therefore be recapitulated here, though with a minimum of detail. The same procedure was followed in the floristic catalogue that appeared as Part I.

The geographic boundaries of the present study are rather arbitrarily drawn (see map, *Fig. 1*). At the south they include the Clearwater River region and the Athabaska River up to Athabaska Landing. Westward they extend roughly to the western borders of the Wood Buffalo Park, and include all of Great Slave Lake. The height of land between Great Slave and Great Bear Lakes marks the northern limit, while at the east the arctic tree line forms the boundary. The arbitrariness of these boundaries is accentuated by the partial and scattered nature of such detailed information as is available. Difficulties of transportation have left huge areas botanically unexplored; and it must be borne in mind constantly throughout the following treatments that the descriptions and conclusions are based upon a relatively small number of samples considering the size of the whole area. It is thought, however, that these samples are fairly representative and that, taken together, they will cover the principal phytogeographic features.

Localities in which more or less detailed studies of vegetation have been made are in most cases the same as those from which I have made collections. Specific data on the positions of these localities will be found in the Introduction to Part I, where latitudes and longitudes are given. For these and other localities mentioned in the following pages reference should also be made to the map (*Fig. 1*).

BOTANICAL EXPLORATION

Our knowledge of the plant life of the Athabaska–Great Slave Lake region began with the observations of the first trader-explorers who found

Hanbury L.
Tyrrell L.
Clinton-Colden L.
Sifton L.
Campbell L.
Ptarmigan L.
L. Eileen
Aylmer L.
Walmsley L.
Artillery L.
Charlton Bay
Far Isld. Pt.
Nonacho L.
Thekulthili L.
Hill Island
Tazin R.
MacKay L.
Bay
McLeod
Christie Bay
Stark L.
Snowdrift R.
Reliance Isl.
King L.
Taltson L.
Deskenatlata L.
Lady Grey L.
Tsu L.
Tazin L.
Charlot Pt.
Leland L.
Fitzgerald
Fond du Lac
Peplar Pt.
Black R.
ATHABASKA
Fishing R.
William
Camsell L.
Lower Corp L.
Taltheilei Nar.
LaLoche R.
Caribou I.
Taltson R.
Tethul R.
SLAVE RIVER
Ft. Smith
Grahot Detour
Salt R.
Gov. Haul Camp
Upper Corp L.
Yellowknife R.
Yellowknife
GREAT SLAVE LAKE
Gypsum Pt.
Resolution
Little Buffalo R.
Buffalo R.
BUFFALO PARK
WOOD
Faber L.
Emile R.
Marian R.
Russell L.
Ft. Rae
Old Ft. Rae
North Arm
Jones Pt.
Windy Pt.
Slave Pt.
Pine Pt.
Buffalo L.
Hay R.
R. la Martre
L. Marian
Deep Bay

Mack.
Kew.
Ont.
Man.
Sask.
Alta
B.C.
Yukon
Alaska
60
62
60

FIG. 1. Map of the Athabaska–Great Slave Lake region.

their way into the Mackenzie basin from Hudson Bay and the Saskatche-
wan.   Samuel Hearne was the earliest of these hardy travelers, arriving at
Great Slave Lake in the winter of 1771–72.   The next was the Saskatche-
wan fur-trader, Peter Pond, who came into the lower Athabaska River
valley in 1778.   White men probably had already settled in the Slave
River country before the traders appeared, though they have left no
written record.   Petitot reports (1885) that the French family name
"Beaulieu" was established in that area when Mackenzie came in 1789.

In the development of botanical knowledge through the years the results
obtained by explorers and travelers can be divided into two categories.
First are those that involved the preservation of actual specimens of plants
as well as botanical descriptions of the landscape, and second those that
contain only the latter.   Of collections there are relatively few.   In the
course of these studies I have seen most of them and have included records
of them in the published Catalogue.   Descriptions containing botanical
notes, on the other hand, are numerous.   In a few instances, such as in
the writings of Sir John Richardson and John Macoun, notes on plant life
are gathered into more or less formal treatments; but in most cases the
information has to be gleaned from careful perusal of survey reports, travel
accounts, and miscellaneous descriptive matter.   In order to be of much
use this kind of material has to be located geographically with reasonable
accuracy — a requirement that is often difficult to meet.   However,
when gathered together and properly evaluated it is surprisingly voluminous
and pertinent.

A fully adequate account of the botanical exploration of the region would
involve, therefore, a brief recapitulation of virtually all of the exploratory
literature.   Such a project not only would become very voluminous, but
would involve a great deal of duplication of material that I have already
published in earlier studies.   The papers, cited above, on the Peace River
region and the Wood Buffalo Park both contain extended bibliographies and
historical discussions.   Another paper, on range conditions in the Park
area (1933), has a similar discussion and an annotated bibliography.
Consequently it is deemed sufficient to present here only a brief summary
of the explorations that have made outstanding contributions to knowledge
of the botany of the region, with particular attention to those dealing with
the country around Great Slave Lake and eastward from the Slave and
Athabaska Rivers.   This will be supplemented by a bibliography for the
whole of the lake district.

Geographic knowledge of the area, with all its botanical aspects, adheres
to a pattern of water trade routes that was set in the early days of explora-
tion and not seriously modified until very recently.   The advent of air
transport is establishing a new pattern, but it is still too early for its effects
to be much felt in the field of biological investigation.   Peter Pond's canoe
route into the Clearwater valley and down the Athabaska River to its delta
(see Wallace, 1929; Innis, 1930) was quickly extended westward up the
Peace and northward down the Slave by Alexander Mackenzie (1801).
The latter carried it across Great Slave Lake to the rich fur country of

the Mackenzie River valley. Because the Mackenzie drains from the western end of Great Slave Lake, the crossing involved only the western arm, either by the south shore or by way of a chain of islands to the north shore and thence westward to the river. These became, and still remain, the principal transportation paths through our region. The western end of Lake Athabaska, at the junction of the Peace and Mackenzie systems, became a vital center for the fur trade, and continued as such for over a century. Nearly all the descriptions written by travelers through the Mackenzie basin contain impressions of the landscapes seen along these main routes, usually to the exclusion of all other parts of the lake country. As a result, precise information about the plant life of the region as a whole has been very slow in taking form.

Before taking up the exploratory history of the various parts of the area, it will be well to mention several papers that have particular value because they are of a general nature. The first of these is Sir John Richardson's account of his Franklin search expedition of 1848–49 (Richardson, 1851; see also Richardson, 1825, 1861). This book is a mine of information on the Mackenzie basin so far as it was known at that time. In addition to a journal of the trip, there are appendices dealing with the phenomena of climate, vegetation, fauna, and aboriginal life. It sums up the great store of knowledge about northwest America that had been accumulating during the period of extraordinary British exploratory activity that occurred in the first half of the 19th century.

Two papers by the pioneer Canadian naturalist John Macoun belong in this category. Both were published as parts of a geological survey report prepared by A. R. C. Selwyn as a result of explorations in 1875. Most of the report is concerned with work in central British Columbia, but Macoun left the main party and returned east by way of the Peace River, Athabaska Lake and River, and the Clearwater. His descriptions of the topography and vegetation of the lower Peace and Athabaska River valleys (Macoun, 1877, pp. 87–95, 110–232) are authentic and clear. They have no equals among the early vegetational descriptions of this or any other part of the Mackenzie basin.

Emile Petitot was a Roman Catholic missionary who traveled widely in the Athabaska–Mackenzie country between 1862 and 1883. He seems to have had an overwhelming interest in geographic matters, which led him not only to keep voluminous notes on the more familiar parts of the region, but also to wander widely in the unexplored wilderness. Beginning in 1875 he published, mostly in France, a long series of books and shorter papers on the country and its people (Petitot, 1875, 1876, 1883, 1885, 1887, 1888, 1891, 1893). Few if any individuals have ever acquired so large a first-hand knowledge of this huge territory, and no one has written more extensively about it. Taken together his works form a veritable eldorado of lore, extremely useful provided one has the patience and knowledge to sift it critically for pertinent and authentic material. Petitot's personal observations appear to be thoroughly reliable, but he so interspersed them

with legend and hearsay that to sort out of them a body of fact often becomes difficult. Furthermore they are commonly interwoven with his own interpretations of natural phenomena which, due to his limited knowledge of the earth and biological sciences, often went astray.

By far the best general biological description of the Athabaska–Mackenzie region was prepared by E. A. Preble (1908). It was based upon three expeditions, the first two under the auspices of the United States Biological Survey, and the third with E. T. Seton. In the summer of 1901 Preble, accompanied by his brother, A. E. Preble, went north by way of Edmonton, Athabaska Landing, and the usual trade route to Great Slave Lake. They remained there until the latter part of July, collecting on the south shore and in the north arm. In 1903 the party consisted of the Preble brothers and Merritt Cary. They went to Resolution at the mouth of the Slave River and there separated, Cary and A. E. Preble going down the Mackenzie as far as Fort Wrigley, and E. A. Preble traveling to Rae and then northward over the height of land to Great Bear Lake. Cary and his companion returned south that season, but E. A. Preble wintered at Fort Simpson and made a trip to the Mackenzie delta in the following year. In 1907 Preble accompanied Seton to the Barren Grounds northeast of Great Slave Lake (see below). Most of the results of these expeditions were zoölogical, but considerable botanical collections were made throughout. Preble's report is especially valuable in the present instance for its careful and thorough descriptions of physical geography, climate, life zones, and exploratory history. Its extensive annotated bibliography was virtually complete for the time in which it was published.

From a geological standpoint, a paper analogous to that of Preble was published by the Canadian Geological Survey, and prepared by Charles Camsell and Wyatt Malcolm (1921). It contains, in addition to a resumé of the geology of the region so far as it was known in 1921, general descriptions of land forms, climate, fauna and vegetation, transportation facilities, and an excellent bibliography.

Three other "source books" should be mentioned. One is the report of a Canadian senate committee appointed to inquire into the resources of the Mackenzie basin in 1888 (See Schultz, 1888); and another is "The Unexploited West," compiled by Ernest J. Chambers (1914). The first contains a mass of miscellaneous information that requires to be winnowed carefully before its actual wealth of first-hand observation can be culled out and organized. The second presents somewhat similar hazards, though it is much more logically arranged in its presentation. Finally there is the excellent little book on "Canada's Western Northland, its History, Resources, Population and Administration," assembled by W. C. Bethune and published in 1937 by the Lands, Parks and Forests Branch of the Canadian Department of Mines and Resources. This volume contains a wealth of authoritative information on northwestern Canada, brought up to date by a corps of men whose experience in that region and its problems is extensive.

CLEARWATER AND ATHABASKA RIVERS

Peter Pond came into the Mackenzie basin by way of Methye Lake, and over Methye Portage to the Clearwater River. This route continued to be the principal one for the fur trade until the 1880's when, with the completion of the Canadian Pacific Railway, a road was established northward from Edmonton to Athabaska Landing. Consequently the Clearwater and lower Athabaska valleys were traversed by nearly all the explorers who came into our region in the first hundred years of its written history. The lower Athabaska, of course, continues to be a central artery of traffic to this day, for the present railhead is on the Clearwater about seven miles above its junction with the Athabaska. Needless to say there is no dearth of descriptions for these routes, since most of the travelers who published anything at all included their impressions of the Clearwater and Athabaska valleys.

In spite of there being so much traffic in these valleys, the number of plant collections from them is very small. No doubt some of Richardson's material came from them, but the labels give no indication of it. Only two collections are of special note. The first was by Robert Kennicott in 1859 (see below), and the second by J. M. Macoun in 1888. The latter traveled down the Athabaska from the mouth of Lesser Slave River to McMurray, then up the Clearwater and over Methye Portage. No separate list of his plants was published, but they were incorporated in John Macoun's Catalogue of Canadian Plants (1883–1890) or its supplements.

This busy route margins one of the least known parts of the entire Mackenzie basin, a vast tract between the Clearwater on the south, the Athabaska on the west, Athabaska Lake on the north, and Cree River and Lake on the east. There appears to be no published description of any kind for this area. Its eastern border was described by J. B. Tyrrell and D. B. Dowling in the course of a geological reconnaissance along Cree River and around Cree Lake in 1892 (J. B. Tyrrell, 1896). Recent aerial photographs and surveys will undoubtedly facilitate its exploration.

LAKE ATHABASKA

A fairly good map of Lake Athabaska was made by Philip Turnor about 1791. Turnor was sent by the British government to establish the position of Fort Chipewyan, a trading post at the west end of the Lake. He traveled from Chipewyan to Stone River near the eastern end and returned, making a rapid survey of the south and north shores en route. His journals, edited by J. B. Tyrrell, were published by the Champlain Society in 1934. An outstanding feature of his map from our standpoint is that it outlines the great sand dune area south of the lake, a feature not subsequently marked upon any map until the most recent ones done by aerial photography. The journals give rather detailed sailing directions, with abundant notes on shore vegetation.

No significant additions to the map of Lake Athabaska were made until 1880 and 1881, when A. S. Cochrane made a survey of the north shore of the lake from east to west (See Alcock, 1936, p. 5). A track survey of the

south shore as far east as William Point was made in 1888 by R. G. McConnell (1893).   In the summers of 1892 and 1893, new surveys of both north and south shores were made by J. B. Tyrrell and his associates, J. W. Tyrrell and D. B. Dowling, of the Canadian Geological Survey. These surveys were part of a larger project which extended eastward to Hudson Bay.   The work of the Tyrrell brothers and Dowling is perhaps the most significant from a botanical standpoint in all the earlier exploratory history of Lake Athabaska.   The principal features of the geological structure of the area were outlined for the first time, and a collection of plants was gathered by J. W. Tyrrell along the entire route of the journey, with extensive notes on vegetation.   The plant collection, determined by John Macoun, contained about 196 species of flowering plants and ferns and about 37 species of cryptogams, many of them from Lake Athabaska. The scientific results of the expeditions were published by the Geological Survey of Canada (J. B. Tyrrell, 1896), while a popular account of the long journey of 1893 was published in book form by J. W. Tyrrell in 1898. In both of these papers the list of plants is included as an appendix.

In 1914 Dr. Charles Camsell of the Canadian Geological Survey led an exploring expedition between Athabaska and Great Slave Lakes by way of the Tazin and Taltson River valleys.   The geological results were published by Camsell two years later (1916).   Attached to this expedition was a naturalist, Dr. Francis Harper, who made collections of both plants and animals.   A brief account of his work was published immediately (Harper, 1915), but his detailed botanical results did not appear until 1931, when a list of the collection was published (Harper 1931–C).   In the same year he also published a paper on the amphibians and reptiles of the region, and another containing a discussion of its biogeography (Harper, 1931–A, B).   His notes on mammals appeared in the following year (1932). Harper again visited Lake Athabaska in 1920, when he traveled eastward along the south shore in company with Dr. Hamilton M. Laing, under the auspices of the United States Biological Survey.   Some plants were collected on this occasion, but no report appears to have been printed.

This concludes the summary of significant botanical exploration around Lake Athabaska prior to our own work, which was begun in 1926.   It is necessary to mention, however, some notable geological papers and topographic maps that have appeared in recent years.   For our purposes the most significant geological reports are by Dr. F. J. Alcock, who spent the summers of 1914 and 1916 on the north shore of the Lake, and who in 1935 was in charge of a large field party in the same region.   His papers on the origin of Lake Athabaska (1920) and on the general geology of its surroundings (1915, 1917, 1936) are of particular interest.   The whole lake area has now been mapped from aerial photographs.   The new maps (Nat. Top. Series, Top. Surv. Can.) show in great detail not only the shore lines and islands of the main lake, but also the complex system of streams and ponds that characterizes the "inland" country.   These maps, especially when they can be supplemented by the photographs themselves, enormously facilitate biological investigation.

REGION BETWEEN ATHABASKA AND GREAT SLAVE LAKES

East of the Slave River valley, and between Athabaska and Great Slave Lakes, is a vast upland of moderate elevation. It is characterized by thin, stunted timber, and by an extraordinary number of lakes. In some places the lakes are so numerous and so close together that the whole surface, as Alcock remarks (1936, p. 7), gives the impression "of a drowned topography with only the ridge summits projecting above the water." No accurate knowledge of any part of this region became available until after Camsell's expedition on the Tazin and Taltson Rivers in 1914. The Tyrrells had skirted its eastern borders in 1893 on their route to Chesterfield Inlet by way of the Black and Dubawnt Rivers (J. B. Tyrrell, 1897), and they were told by the Indians of the track later used by Camsell. Strangely enough, a rather accurate account of the main canoe routes through the upland was written many years before, purely from Indian reports. Richard King, who was surgeon and naturalist to Back's expedition in 1834 (see below), wrote a personal account of his journey which was published separately (1836). During the planning of Back's journey the Indians had urged the use of a canoe route through the country southeast of Great Slave Lake. The Indians said that this would lead into a north-ward flowing river from which the arctic watershed could be reached. King published an Indian sketch map of the route at the close of his narrative. The Back expedition chose the eastern arm of Great Slave Lake, however, and the Indian route was not investigated until 1925, when G. H. Blanchet of the Canadian Topographic Survey followed it through to the Thelon River (Blanchet, 1926–C). Starting from Fitzgerald on the Slave River he crossed the upland in a northeasterly direction through a long series of lakes, streams and portages to the upper Thelon, then returned by way of the Snowdrift River and Great Slave Lake.

Blanchet made another journey in this general region in 1926. On this occasion he set out from Tazin Lake in an attempt to find a route into the Thelon, but after a long and difficult journey northeastward over a broad height of land he found himself in the Dubawnt drainage by which he returned to the Black River and Lake Athabaska (Blanchet, 1927).

Except for the material gathered by Harper in 1914 (see above), detailed botanical information on the upland east of the Slave River is practically non-existent. From Blanchet's notes it is possible to place on the map a few facts about the distribution of forest types, but otherwise the country remains to be explored.

GREAT SLAVE LAKE AND THE LOCKHART BASIN

In spite of the fact that a major trade route led through Great Slave Lake from Mackenzie's time on, details of the geography of the whole lake were not available for many years. In fact some glaring inaccuracies, particularly as to the eastern arm, remained on the maps until 1926, when the first comprehensive government survey was made. Even today, in some of our standard atlases, the corrections have not yet been entered. The first known description of the lake was written by Samuel Hearne (1795),

who crossed the eastern arm from north to south in the winter of 1771–72. He called it "Athapuscow Lake," and for a long time it was thought that he actually crossed Lake Athabaska; but studies of his track made by D. B. Dowling (1893) and J. B. Tyrrell (1911) show clearly that he came overland from the Coppermine River by way of Mackay Lake, crossing Great Slave Lake in such a way as to arrive on the south shore at a point not far east of the Slave River delta. Earlier in the season, on his way northeastward to the Coppermine, he passed through the Lockhart basin, probably just east of Artillery Lake.

Mackenzie's description (1801) of the western arm was written in 1789, when he made his remarkable journey down the Mackenzie River, but he was preceded at Great Slave Lake by a trader named Leroux, who built a house near the eastern side of the Slave delta in 1786. There is also some evidence that associates of Peter Pond had a trading establishment in the same locality as early as 1781 (see J. B. Tyrrell, 1934, p. 518). Leroux also built a post in the north arm, probably near the present site of Rae, about 1789.

The earliest plant collections from Great Slave Lake were made by John Richardson, surgeon and naturalist to the Franklin expeditions of 1819–22 and 1825–27 (See Franklin, 1823, 1828). They came from the west and north arms of the lake, but specific localities are lacking on most of their labels. On the first journey the party went to Yellowknife Bay on the east shore of the north arm, and ascended Yellowknife River to a height of land by which they reached Point Lake and the Coppermine. They returned to Slave Lake by the same route after a trip down the Coppermine and eastward along the arctic coast, and after a disastrous adventure on the way back through the treeless country northeast of Point Lake. Most of the second expedition was devoted to surveys of Great Bear Lake and the arctic coast west of the Coppermine, but some plants were collected at Great Slave Lake. Botanical results of the first expedition were published by Richardson in an appendix to Franklin's narrative of that journey (Franklin, 1823); and the material from both expeditions later became the basis for a large proportion of the classic "Flora Boreali-Americana" by W. J. Hooker (1840).

The Franklin Expedition specimens were all placed in the herbarium of the British Museum, from which duplicates were from time to time sent to America. A large number of these came to Asa Gray and John Torrey during the period when Torrey's "Flora of North America" and Gray's "Synoptical Flora" were being prepared. As a result they are now more or less concentrated in the Gray Herbarium and the Herbarium of the New York Botanical Garden, although a considerable number are in the National Herbarium of Canada. Another group was acquired by John A. Lowell of Boston, and these were at the Boston Society of Natural History until recently, when they were moved to the Gray Herbarium. The latter institution now has by far the best representation in America of the early Mackenzie basin collections, as well as of the Arctic and Rocky Mountain material that formed the basis for "Flora Boreali-Americana."

The first extensive descriptions of the eastern arm of Great Slave Lake were made in 1833 and 1834 on the occasion of Capt. George Back's expedition (Back, 1836; King, 1836). Back's party traveled northward by the Slave River, and through the eastern arm of the lake to its extremity, where they established Fort Reliance as winter quarters. From here they went northeastward through the lake country of the Lockhart River basin, and across a height of land to Back River, which they descended to the arctic coast. Only a few plants were collected on this expedition, but the published narratives and appendices are replete with notes on topography and vegetation.

Captain W. J. S. Pullen of the British Navy came southward through our region in 1852, collecting a few plants along the upper Mackenzie and possibly along the western arm of the lake (Pullen, 1852). He had been engaged in the search for the lost Franklin Expedition, and had spent the two preceding winters at Fort Simpson. A list of his plants is to be found in the Botany of the Voyage of H. M. S. Herald (Seemann, 1852–57). It was in the 60's and 70's that Emile Petitot was gathering material for his extensive writings on the geography of the Mackenzie basin. His map of Great Slave Lake is surprisingly accurate considering the limited means of surveying at his disposal. Richardson's account of his Franklin Search Expedition of 1848–49 should also be mentioned here, although it did not contain much specific description of Slave Lake. An early attempt to penetrate the upland north of McLeod Bay, in the eastern arm, was made in the summer of 1855, when James Anderson (1856) of the Hudson's Bay Company went northward by canoe from near Mountain River. He followed a chain of lakes that brought him to Lake Aylmer, and then returned to McLeod Bay by another route farther east.

Strangely enough one of the most important plant collections ever made in the Mackenzie country dates from this period, though no account of it was ever published. It was the work of Robert Kennicott, who made a long journey down the Mackenzie and into the Yukon valley in 1859 and 1860 under the auspices of the Smithsonian Institution and the Chicago Academy of Sciences. Not only did Kennicott himself gather large collections of both plants and animals along the Athabaska, Slave and Mackenzie Rivers, but he so inspired Hudson's Bay Company officials in the region that they continued to send material to the Smithsonian for many years thereafter. The zoölogical collections were studied and published upon many years ago by E. A. Preble (1908), but the plants were never listed until 1936, when I incorporated those from our region in the Catalogue. Most of the plant specimens are now in the herbarium of the New York Botanical Garden. A biography of Kennicott containing his northern itinerary was published by the Chicago Academy of Sciences in 1869.

The maps of shores in the western and northern arms of the lake were somewhat improved by William Ogilvie in 1887–88 (1890), and by R. G. McConnell (1891). McConnell wrote some excellent descriptions of the topography in the country around the western arm, pointing out the possible

significance of the old terraces above the present shore. Also he made overland trips between Rae and Providence, and he is one of the very few people who have described the semi-open country in that district.

A few descriptive notes on the eastern arm of Great Slave Lake and the Lockhart basin were written by James McKinlay in 1890, in the course of a trip from Resolution to Beechy Lake on Back's River. The material is in the form of a diary, edited and published by D. B. Dowling in 1893.

In the summer of 1892 Elizabeth Taylor traveled through the country by the usual trade routes, making numerous zoölogical and botanical collections. Although I have been unable to find any published narrative of her journey, her collections of plants are well preserved and bear excellent data as to localities and dates. They are distributed among the herbaria at the National Museum of Canada at Ottawa, the New York Botanical Garden, and at Harvard, while a few have found their way into other institutions. Unfortunately, most of the collection was originally numbered serially by specimens, with some duplication and omission of numbers, so that duplicates cannot now be recognized from the numbers on the labels.

A number of sportsmen and explorers passed through Great Slave Lake during the 1890's, but for the most part they contributed little to our knowledge of the vegetation. A notable exception was Frank Russell, a zoölogist from the University of Iowa, who spent the seasons of 1893 and 1894 in the Mackenzie basin. The first part of the summer of '93 was spent in the Athabaska delta; then he went to Rae and used that as his base of operations until May of the following year. He made several long hunting trips from Rae, among them one to Providence overland. His report, published in 1898, contains many useful botanical observations. Warburton Pike traversed the eastern arm of the lake in 1889 and again in 1890, on hunting trips to the Barren Grounds. His narrative, published in 1892, has been one of the most widely read books of travel in northern Canada. Others whose primary interest was big-game hunting were Henry T. Munn, who went into the country east of Slave Lake in the summer and fall of 1894 (Munn, 1932), and Caspar Whitney, who spent the winter of 1894–95 hunting with the Indians eastward from Rae (Whitney, 1896). Another colorful figure to appear on the scene about this time was "Buffalo" Jones. He and a companion named Rea, in the summer of 1897 and in the following winter, made a vain attempt to secure live musk-oxen from the region northeast of Fort Reliance. Jones himself published no account of his adventures, but entertaining descriptions of them were written by Emerson Hough (1898) and Henry Inman (1899).

The first comprehensive geological investigations around Great Slave Lake were made in 1899 by Robert Bell and his assistant J. M. Bell of the Canadian Geological Survey (R. Bell, 1900; see also J. M. Bell, 1929). They made track surveys of Christie and McLeod Bays in the eastern arm and of parts of the north arm. Their report contains many significant botanical observations and valuable notes on the post-glacial shore lines that are so closely related to the history of the vegetation.

In 1900 J. W. Tyrrell, under the auspices of the Canadian Department of Interior, made a remarkable journey from Great Slave Lake to Chesterfield Inlet and return. His report (1902) includes appendices giving many valuable meteorological and geographic data and a list of 83 species of plants collected. While most of the material concerns the country beyond the Lockhart basin, there are some significant notes on the eastern arm of Great Slave Lake and on Artillery Lake.

Some notes on arctic vegetation and the geography of the timberline northeast of Great Slave Lake are found in the travel narratives of David T. Hanbury (1900, 1903, 1904). Hanbury first came into our region in 1899 from Chesterfield Inlet. He traveled up the Thelon River, crossed to Artillery Lake, and reached Great Slave Lake by way of the Lockhart River. In 1901 he went eastward from Resolution through the eastern arm and Artillery Lake, and over the height of land to the Hanbury River, which he descended to the Thelon.

E. A. Preble's important work in 1901 and 1903–04 has already been discussed, but his journey with E. T. Seton in 1907 should have special mention. The description of this expedition was published by Seton in 1911, in one of the most charming books of travel in the Athabaska–Great Slave Lake region that has appeared. It is filled with lively descriptions of the plants and animals encountered, and of the people and their life. Its account of the summer pest of mosquitoes and flies is second to none. A list of plant collections is given in an appendix, and most of the specimens are in the National Herbarium of Canada.

A few notes on the vegetation of the eastern arm of Great Slave Lake are to be found in the report of E. A. Pelletier published in 1910. Pelletier was an Inspector in the Royal Northwest Mounted Police who made a journey in 1908 through the Athabaska and Great Slave Lake country and to Chesterfield Inlet by way of the Lockhart basin and Thelon River.

A few data on the country east of Rae were published by David E. Wheeler in 1914. Wheeler made two trips in this area, in 1910 and 1913. On the latter he traveled as far east as Clinton-Colden Lake in the Lockhart basin.

Geological survey work was carried out in 1916 by A. E. Cameron in the country south of the western arm of the lake. Some excellent notes on topography and vegetation are found in his reports (1917, 1918, 1922–B), and they are of particular interest here because they were the beginning of the field studies that led to Cameron's discussion of the post-glacial lakes of the Mackenzie basin (1922–A). This paper has proved extremely stimulating for investigations of vegetational development.

The discovery of oil along the lower Mackenzie led to greatly increased geological survey activity throughout the Mackenzie valley and around the western arm of Slave Lake. Papers of significance for our purposes were prepared by G. S. Hume (1921) and A. E. Cameron (1922–B), both of the Geological Survey of Canada. New geological maps were made for most of the western arm, and for part of the west shore of the north arm. A number of small plant collections were gathered from time to time by

members of the field parties under Cameron and Hume.   These collections are in the National Herbarium of Canada and are incorporated in the Catalogue.

Some descriptive matter on the eastern arm of the lake was written by J. C. Critchell-Bullock in 1925.   An account of his journey, mostly in the country northeast of the lake, was published in 1931.   It contains a great deal of miscellaneous data on vegetation, animal life, weather, and seasonal changes.

About 1924 the Topographical Survey of Canada undertook to make new maps of the complex shores and islands of Great Slave Lake and the Lockhart basin.   G. H. Blanchet was placed in charge of the work, and during his extensive travels he made voluminous notes on topography, geology, and natural history.   These were published in three papers (1925, 1926–A and B) filled with authentic, first-hand information on a great variety of subjects of interest to the bio-geographer.   A few geological notes by W. L. MacDonald appear as an appendix to one of these papers (1926–A).

Two geologists, George M. Douglas and Carl Lawson, spent the summer of 1928 investigating the southern shores and islands of the eastern arm. Douglas' account of the trip (1929) contains the narrative, while a paper by Lawson (1929) gives a description of the geological findings.

The Geological Survey of Canada began further investigations in 1929 at Great Slave Lake, with a field party in charge of C. H. Stockwell. Between 1929 and 1931 all the country immediately around the eastern arm was studied, and in 1932 Stockwell made a reconnaissance trip up the Yellowknife to the Coppermine, then east to Thonokied Lake and south to the eastern arm of Slave Lake.   Stockwell's report (1933) has much information on glaciation and plant life that is useful for present purposes. The discovery of gold in the Yellowknife Bay area has greatly stimulated geological survey activity around the north arm.   Papers by F. Jolliffe (1936), C. S. Lord (1939), J. F. Henderson (1938, 1940), and A. W. Jolliffe (1939) contain some of the results of this work.   One of the members of Stockwell's party of 1929 was H. W. Fairbairn, an amateur naturalist who later published (1931) a paper on the birds and mammals seen during that summer.   He included a few notes on forest types.

Two recent papers on the region northeast of Great Slave Lake are of particular significance to biologists.   The first is by W. H. B. Hoare (1930), and results from his extensive travels while studying grazing conditions for musk oxen and caribou.   The second reports a general biological investigation of the Thelon Game Sanctuary by C. H. D. Clarke (1940). This paper contains extensive observations on timberline vegetation in the region of Artillery Lake and on the Thelon River.

Region West of the Slave and Athabaska Rivers

Summaries of the exploration of this part of our region will be found in my earlier papers (1933, 1934, 1935) and need not be repeated.   Attention should be called, however, to an excellent recent article by J. D. Soper

on the Wood Buffalo Park (1941). This paper is devoted to the "History, Range, and Home Life of the Northern Bison," and contains significant additions to our knowledge of the plant geography of the Park.

TOPOGRAPHIC FEATURES OF THE
ATHABASKA–GREAT SLAVE LAKE REGION

The Athabaska–Great Slave Lake region may be divided topographically into four provinces which are reflections of major events in its geologic history. They are: the Caribou and Birch Mountain Plateaus, the Alberta Plateau, the Laurentian Plateau, and the Mackenzie Lowland. These divisions were first outlined by Camsell and Malcolm in 1921.

The Caribou and Birch Mountains are isolated plateaus of Cretaceous rock in the southwestern part of the area. The former reach an altitude of about 3500 feet, and the latter about 2300 feet above the sea. The Thickwood Hills west of McMurray are of similar nature. These plateaus are the highest land surfaces to be found in our region. Very little descriptive matter concerning them has ever appeared, but judging from a few scattered notes and from my own observations in the Wood Buffalo Park, they are rather flat-topped, with margins deeply dissected by rapid streams (Raup, 1935). Similar outlying plateaus elsewhere in the Mackenzie basin are the Buffalo Head Hills and the Eagle, Horn, and Watt Mountains.

The Caribou Mountains lie between the lower Peace River and Buffalo Lake. Eastward they extend into the Wood Buffalo Park, and westward to the valley of Hay River. The Birch Mountains are immediately west of the lower Athabaska River and south of the Birch River. The surfaces underlain by Cretaceous rock, of which they are the highest part, are to be seen on both sides of the Athabaska above the Firebag River, and in the McMurray district they form high bluffs along the main streams.

Stretching northward and eastward from the Caribou and Birch Mountains is the Alberta Plateau. It is a gently rolling plain, rather poorly drained, and characterized by morainic ridges, outwash plains, and glacio-lacustrine deposits. Its northern boundary, west of the Slave River, is indicated by a well-defined escarpment making a fall-line for streams draining in that direction. In our area this fall-line appears in the region southwest of Fort Smith, where it is known locally as Salt Mountain. From there it trends in a northwesterly direction into the northern part of the Wood Buffalo Park, then southwesterly to cross the Buffalo River drainage above Buffalo Lake and Hay River at Alexandra Falls. The elevation of the plain southwest of Fort Smith is about 1100 feet. Camsell and Malcolm (1921, pp. 17–18) consider the Alberta Plateau to be a part of the northward extension of the great central plain of the continent: "It corresponds to the second and third prairie steppes in the Great Plains region south of the height of land. . . ." They point out that the "surface rises gradually southwest and west to the foothills of the Cordillera. The slope, however, is so gradual that the smaller streams which have not the power to cut graded valleys from the plateau to the lowland, are comparatively sluggish in the plateau and are rapid and broken only where they

descend through the escarpment. The surface, therefore, is monotonous and outcrops of the solid rocks are rare, and because the drainage is immature, muskegs are abundant and lakes fairly numerous." In our area the Alberta Plateau is underlain by Paleozoic shales and limestones. Some of the latter are highly gypsiferous and cavernous, giving rise to an extensive sinkhole topography. For further discussion of its physical features and soils see Camsell, 1903; Raup, 1933, 1935; Soper, 1941.

Approximately the northeastern half of the Athabaska–Great Slave Lake region lies in the Laurentian Plateau. This is one of the major physiographic provinces of the continent, extending eastward to Labrador. Nearly all of Lake Athabaska lies within it, as well as the eastern arm and the eastern shore of the northern arm of Great Slave Lake. In characterizing it I can do no better than quote parts of Camsell and Malcolm's description (1921, pp. 11–14).

"The western border of this province, where it abuts against the central plain, is a fairly well-defined line marked by the contact between the Precambrian crystalline or metamorphic rocks and the flat-lying Palaeozoic sedimentary rocks. The line of contact enters the Mackenzie basin from the south at Methye portage on Clearwater river in longitude 110 degrees west. Running northwesterly from there it passes the west end of Athabaska lake and follows the valley of Slave river to Great Slave lake. Crossing Great Slave lake in northwesterly direction it runs from the northern end of the north arm of the lake to the southern point of McTavish bay on Great Bear lake. . . ."

"The physical features of this province are typical of the whole Laurentian plateau generally. When viewed broadly the topography is that of a broad plain sloping gradually to the west and north with a gradient towards the great lake depressions which rarely exceeds 6 or 8 feet to the mile. Here and there residual round-topped hills or monadnocks rise a few hundred feet above the general level, but these hills are not as a rule connected into definite ranges nor aligned in any particular direction. In detail, however, the plateau is very irregular, broken, and rocky, with an uneven hummocky or mammillated surface." "The greatest relief is found on the shores of the great lakes where it reaches a maximum of about 1,000 feet." The maximum altitudes above sea-level for the various parts of our region do not vary greatly. Camsell and Malcolm give the following figures: at Cree and Wollaston Lakes, 1650 feet; on the north shore of Lake Athabaska, 1490 feet, at Great Slave Lake, 1520 feet; and on the divide between Great Slave and Great Bear Lakes, about 1700 feet.

"The Laurentian plateau portion of the Mackenzie basin is essentially a lake country, and its surface is covered with thousands of lakes of all sizes, ranging from mere ponds to lakes hundreds of square miles in extent. So numerous are these lakes and so rocky and irregular the country between them that the only method of travel used by the natives or travelers in summer in this region is by canoe. By portaging from one lake to another it is possible to travel by canoe in almost any direction required. . . ."

"[The lakes] are usually very irregular in outline and their shape and alignment have been determined partly by the structure and composition of the rocks in which they lie and partly by the direction of movement of the glacial ice-sheet."

"The Laurentian plateau in the Mackenzie basin has as a rule little or no mantle of soil or other loose material covering its bedrock. . . . A very large proportion of the region has a rocky surface. Boulder clay is found frequently filling depressions on the surface and here and there occur sand plains or other accumulations of glacial drift. The whole region has been subjected to intense glacial erosion by which the surface has been worn down to the live rock and denuded of its loose material which has been carried westward and deposited in the lowland portion of the basin. South of Athabaska lake is a large area underlain by horizontally bedded sandstone which on decomposition forms wide plains of sand or gently rounded hills and ridges. . . ." The youth of the surface, together with the scarcity of finely divided materials, have resulted in highly disorganized drainage systems, with clear water in the lakes and streams.

The Mackenzie Lowland province is represented in our region by a low plain around the western arm of Great Slave Lake, with long extensions up the valley of the Slave River and into the lower valleys of the Peace and Athabaska. Nowhere does its surface rise much above the levels of the main streams and lakes. According to Camsell and Malcolm (1921, p. 20), "The elevation of the lowland at the west end of Athabaska lake is about 700 feet above the sea and the slope of the surface from that point to the Arctic averages about 8 inches to the mile. . . ."

The surface of the lowlands is a rather monotonous flat plain made of alluvial or glacio-lacustrine soils. There are many shallow, marshy lakes and meandering, sluggish streams. Soils on the banks of the larger rivers are well-drained and suitable for a limited agriculture, but the back country holds vast expanses of muskeg and swamp. The main streams, such as the Peace, Slave, Little Buffalo, Buffalo, and Hay Rivers, wind through broad flood plains with many islands, bars, and abandoned channels.

As will be shown later, the boundaries between the four physiographic provinces just described are coincident with some of the principal floristic and vegetational boundaries in this region. This is particularly true of the border of the Laurentian plateau and of the margins of the Cretaceous uplands. The Alberta Plateau escarpment is also significant botanically, as I have pointed out elsewhere (1935). Some further elaboration and subdivision of the four provinces becomes necessary when their surface geology is examined.

GEOLOGY AND SOILS

Introduction

The contribution of geological science to the study of vegetation may be said to be three-fold. First, it offers a rational explanation for the topographic patterns with which maps of vegetation or of species are commonly correlated; and at the same time it outlines geomorphic processes to account for change in topography and, in many cases, for change in vegetation.

Second, it supplies the basis for the study of origin, distribution, and development of soils. And third, it outlines sequences of events in the formation of topography and soils, with time scales of greater or lesser accuracy, which may be related to suspected sequences in the development of the plant cover. It may be said that within broad limits the positive correlation of vegetation patterns with those of topography and soils, especially the latter, is inversely proportional to the length of time during which the surfaces and soils have remained unaltered by major geomorphic events. This is based upon the theory in modern soil science that, given time enough, soils and vegetations tend to become uniform under given climates, regardless of the geologic origins of the soils.

The soils and surfaces of the Athabaska–Great Slave Lake region are for the most part youthful in terms of time and soil-forming processes. Most if not all of them have been exposed for the acquisition of vegetation only since the retreat of the last glacier or of its adjacent lakes. A positive correlation should be expected, therefore, between the distribution of vegetation and the patterns of geologic features. Although the final episodes of the last glaciation are of outstanding significance, it is necessary to look first at the distribution of the major kinds of bedrock, for they determine in large measure the amount and condition of the existing soils, whether the latter are of glacial origin or have weathered from the rocks since they were exposed.

In the present state of our knowledge of the relations between rocks and vegetation in this region, it will be unnecessary to describe the rock formations in detail. Of greatest importance are the relative rates at which the rocks have produced soils, and, in general terms, the history, position, and physical and chemical properties of these soils. *Figure 2* is a map showing the surface distribution of principal rock formations.

PRE-CAMBRIAN FORMATIONS

The topographic province of the Laurentian plateau is in our region composed entirely of pre-Cambrian rocks. The oldest of these rocks are variously metamorphosed sedimentaries usually considered to be of early pre-Cambrian (Archean) age. These ancient sediments are widely scattered in the country north of Lake Athabaska and around the eastern arm of Great Slave Lake. North of Lake Athabaska they are known as the "Tazin Group," and are composed of "dolomite, limestone, quartzite, argillite, conglomerate; mica schist and gneiss; volcanic flow and fragmental rocks" (Alcock, 1936, p. 10). These rocks are commonly found in small masses, and are surrounded and much intermingled with younger magmatic granites and granitoid gneisses, the welling up of the magma having caused the disruption and alteration of the sediments. About the eastern arm of Slave Lake, rocks thought to be of similar age are called the "Point Lake–Wilson Island Group." They include "conglomerate, arkose, quartzite, phyllite, dolomite, specularite iron formation, gneiss, schist, basalt, andesite, trachyte, and rhyolite" (Stockwell, 1933, p. 46). They likewise are highly altered by granitic intrusives.
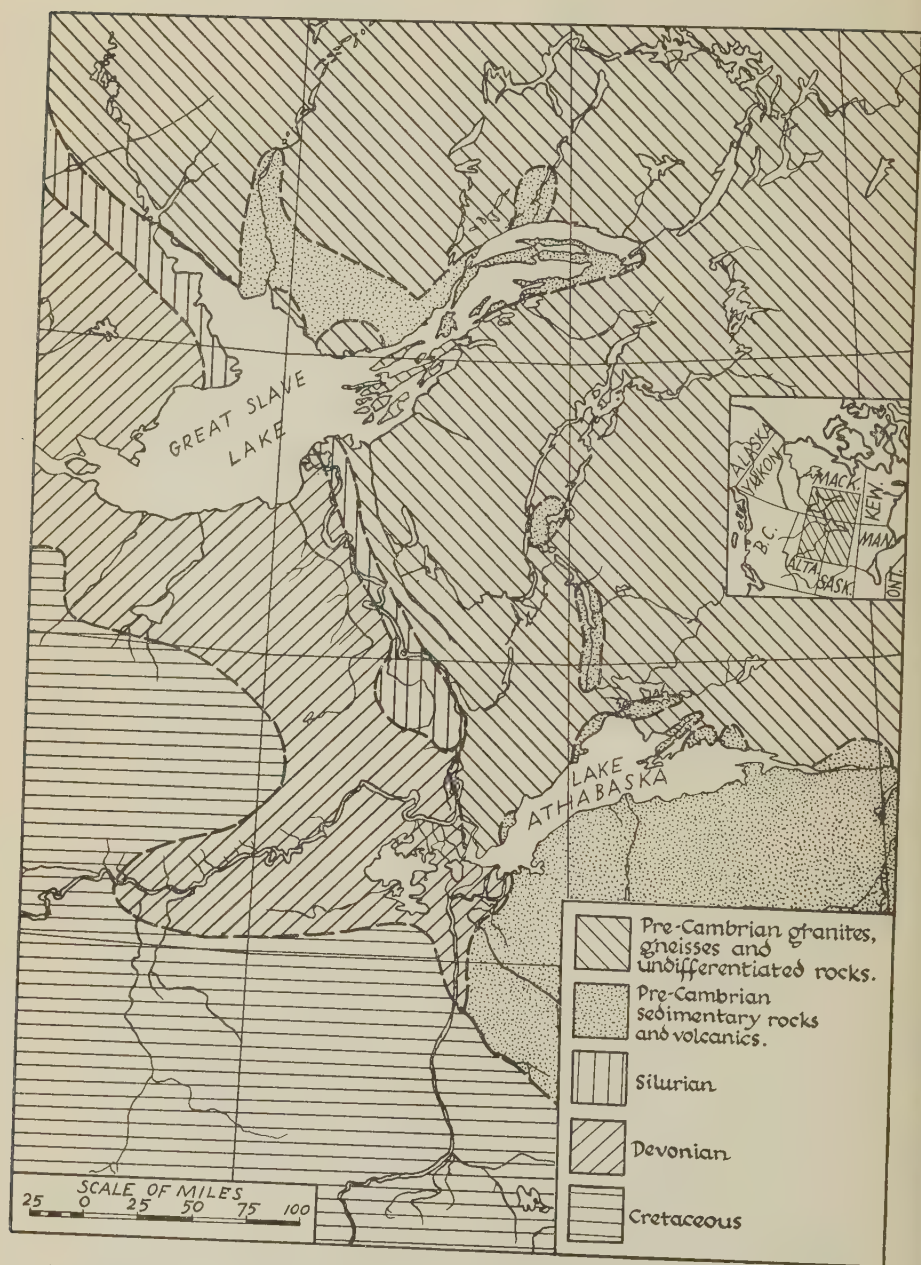
Fig. 2. Map of the principal geological formations in the Athabaska–Great Slave Lake region.

Above the Archean rocks is an unconformity and then come late pre-Cambrian (Proterozoic) deposits characterized by conglomerates, sandstones, quartzites, shales, and volcanic intrusives. One group near the base of this section at Great Slave Lake contains some dolomites and limestones. North of Athabaska Lake the oldest of the late pre-Cambrian groups is composed of quartzite, conglomerate, and iron formation, and is known as the "Beaverlodge Series" (Alcock, l. c.). It is much altered by basic intrusives and some granite, and is topped by an unconformity and finally by the "Athabaska Series" of "conglomerate, arkose, sandstone, shale. Balsalt flows and dikes."

Late pre-Cambrian formations at Great Slave Lake as described by Stockwell (1933, pp. 55–60) have at their base the "Great Slave Lake Group" of sediments and volcanics. There is a great variety of rocks in this group, including conglomerates, sandstones, shales, slates, dolomites, and limestones. They are disrupted and altered by dioritic intrusives. Above them is an erosional unconformity, followed by another group of sediments called the "Et-Then Series." This series, composed of conglomerates, sandstones, and quartzites, is thought to be of the same age as the Athabaska Series. Still later intrusives of diabase cut the Et-Then rocks.

By far the most widespread of the pre-Cambrian rocks, in surface exposure, are the Archean granites and granitoid gneisses, and the late pre-Cambrian sandstones and quartzites. The former are the rocks most commonly seen in the vast country between Athabaska and Great Slave Lakes and in the region around the eastern arm of Great Slave Lake. The latter predominate south of Lake Athabaska and apparently underlie most of the lake itself, for they outcrop on the islands and in places on the north shore. Scattered throughout the granitic areas are the older and younger sediments and intrusives.

When translated into terms of immediate significance to plant distribution, these rock formations may be correlated with a rough phytogeographic boundary at the north shore of Lake Athabaska. Northward from the boundary most of the surface is of hard granitic rocks so resistant to weathering that they have produced scarcely any soil since they were cleaned off by the last advance of the glacier. Most of what soil there is has developed from local till deposits, small alluvial beds, or peat accumulations around lakes. Southward from the boundary are sandstones and quartzites that have weathered more rapidly to form extremely light sandy soils in post-Glacial time, or have been the origin of sandy outwash from the glaciers themselves. In the granitic country is a third kind of surface which, though scattered and often of small extent, is none-the-less distinctive. Its rocks have weathered faster than either the granites or the sandstones, and in many places have produced a thin residual soil in the short time since they were exposed. Most conspicuous in this respect are the limestones, shales, and dolomites of the Tazin and Et-Then Series and of the Great Slave Group. Intermediate between the softer rocks and the

Athabaska sandstones are the conglomerates of all the sedimentary series.

Botanical effects of these major variations in rocks and soils are seen at once in the landscapes of the Laurentian Plateau. South of Lake Athabaska are broad plains and rounded hills of sand and gravel, while on the south shore of the lake itself are many miles of shelving sandy beaches backed by a complex array of sand ridges and terraces with here and there outcrops of flat-lying sandstones. Immediately south of the shore are huge areas of shifting dunes. Sand beaches are also characteristic of many parts of the north shore, particularly toward the western end of the lake. Sand beaches and sandy plains also appear on Great Slave Lake wherever there are large outcrops of the sandstones of the Great Slave Lake group or of the Et-Then Series, such as in the Snowdrift River and Fort Reliance areas. The granitic country is a dreary waste of stunted, scattered timber, with a large total area of rock that is covered only by lichens, mosses, and a few herbaceous or shrubby plants that cling to the rock surfaces or find small pockets of soil in crevices and glacial till. Scattered through it are what might almost be called oases, where the rounded hills are green with grasses and sedges, and the slope and valley forests are of well-formed trees. These are the limestone and dolomitic outcrops whose surfaces have been broken by frost and subaerial weathering to form thin but rich, fine-textured soils. In addition to their fineness in texture, these soils have a chemical composition that attracts calcicolous species of plants, thereby further enriching their flora.

Botanical correlations with the principal rock differences just described are to be found also in the distribution of lake shore and pond vegetation, and in the arrangement of forest types over the landscape. Further discussions along these lines will be found in other parts of this paper.

PALEOZOIC FORMATIONS

The physiographic provinces of the Alberta Plateau and the Mackenzie Lowland are underlain, so far as is known, by Paleozoic rocks of Silurian and Devonian age. These rocks are relatively undisturbed, flat-lying, and composed principally of dolomite, limestone, and shale. The present surface materials, as previously stated, form a mantle of till, outwash, glacio-lacustrine, and alluvial deposits which so cover the bedrock that few exposures are seen. Those studied by geologists are along the lower Athabaska and Peace Rivers, at a few places along the Slave River and around the western shores of Great Slave Lake, in the valleys of Hay and Buffalo Rivers, and at several places along the Alberta Plateau escarpment.

Silurian deposits are principally represented in our area by a formation called the Fitzgerald Dolomite (See Camsell, 1917; Cameron, 1922–B). It consists of gray dolomitic limestone with gypsum and anhydrite. Exposures of it can be seen along the Peace River near Little Rapids and at Peace Point, at several places along the Slave River, in the escarpment southwest of Fort Smith, and at Gypsum Point on the northwest shore of Great Slave Lake. Extensive sink-hole development over these beds indicates their gypsiferous nature, and an elaborate system of underground drainage appears to have been set up in them. Salt springs issue from

them in some places, particularly south and west of Fort Smith, where nearly all of the surface water immediately below the Salt Mountain escarpment is brackish.   On the basis of their high gypsum content, and to some extent on fossil evidence, these dolomites have been placed in the Upper Silurian.   Some red beds of calcareous shale, red gypsum, salt, and red arenaceous shale have been found beneath them at Gypsum Point, however, and are also classed as Silurian.

The lower Devonian does not appear to be represented in our region, but on the south and north shores of the western arm of Great Slave Lake Middle Devonian rocks outcrop in many places (Cameron, 1921).   These rocks have been divided, on lithological and fossil grounds, into three groups, called the Pine Point Limestones, Presqu'ile Dolomites, and the Slave Point Limestones.   They vary from soft shaly limestone to hard crystalline dolomite.

Upper Devonian strata are widespread around the western extremity of Great Slave Lake and along the upper Mackenzie.   They appear in the Hay and Buffalo River sections, and at Vermilion Chutes on the Lower Peace River.   It is assumed that they underlie most of the Alberta Plateau southwest of Great Slave Lake.   Although they contain some limestones, most of them are shales.   In our region they are divided into the Simpson Shales, the Hay River Shales, and the Hay River Limestones.   Along the lower Athabaska River are gently arching beds of limestone that are commonly seen on the banks between McMurray and the Firebag River. These are generally regarded as of Upper Devonian age, possibly to be correlated with the Hay River Limestones.

The phytogeographic significance of the Paleozoic formations results in large measure from their attitude and relative softness.   Being nearly horizontal, they offered but little resistance to glacial movement; and upon the retreat of the ice they presented a series of comparatively level plains upon which till and outwash could be widely spread, and upon which broad lake deposits could be laid down.   At the same time they were composed of rocks sufficiently soft for the formation of thick deposits of glacial debris. Other botanical aspects are significant locally.   The presence of the limestones has encouraged a certain amount of calcicoly in the flora, apparent chiefly near actual outcrops or in ponds and lakes.   The saline springs from the Silurian formations have already been mentioned.   The spread of their waters over the "Salt Plains" south and west of Fort Smith has given rise to a halophytic flora containing many species uncommon or unknown elsewhere in the region.   Another aspect of great importance in the country immediately underlain by Silurian rocks is in the peculiar topography and drainage of the sink-holes.   Many of them are dry, but others contain ponds whose levels are apt to fluctuate widely and lead to extraordinarily complex vegetational development (See Raup, 1935).

CRETACEOUS FORMATIONS

Cretaceous rocks underlie most of the southwestern uplands of our region, comprised in the Caribou and Birch Mountain Plateaus as well as

in the uplands around McMurray and the Clearwater River. They have been studied chiefly along the lower Athabaska and Peace Rivers, and in the valley of the Hay River. I shall make no attempt to describe the entire sections in these areas, but will mention only the formations immediately concerned with our region.

One of the most striking features of the landscape in the Clearwater–McMurray district is the thick deposit of "Tar Sand" that forms the bluffs along the rivers. It is a highly bituminous sandstone called the McMurray Formation (McLearn, 1917; Camsell and Malcolm, 1921), directly overlying the Devonian limestones. It is black in color and contains so much petroleum that on warm summer days it becomes viscous where exposed to the sun. Along the Athabaska just above McMurray it is overlain by gray or black shales and gray or green sandstones of the Clearwater Formation. This and four other Cretaceous formations are to be seen along the Athabaska within 75 miles above McMurray, and they have also been noted in the valley of Moose River, a small western tributary that comes into the Athabaska near McKay. These formations are the Grand Rapids Sandstone, Pelican Shale, Pelican Sandstone, and La Biche Shale.

On the Peace River at Vermilion Chutes are outcrops of the Loon River Shales which are correlated with the McMurray and Clearwater Formations of the Athabaska section (McLearn, 1918). Likewise on the Hay River Cameron (1922–B) has described marine shales that he has correlated tentatively with the Loon River Formation. Although the Caribou Mountain Plateau has not been explored by geologists, it is presumed to contain a Cretaceous section analogous to those of the Athabaska and Peace Rivers.

The full botanical significance of the Cretaceous uplands is not yet known. Their elevation must have a profound effect upon their climates, while their soils, whether glacial or residual, differ widely from those in other parts of our region. It is known that they harbour outliers of Cordilleran or foot-hill vegetation, and their northern and northeastern margins have already been noted as a prominent floristic boundary (Raup, 1930). Whether or not they were entirely covered by the latest advance of the Pleistocene ice remains to be checked. I have seen some clayey soils high on the eastern slopes of the Caribou Mountains that appeared to be residual. In any case the upper parts of the plateaus must have been the first land in our region to be exposed for plant cover after the retreat of the ice. By their height and position the Cretaceous plateaus had a large influence upon the direction of movement of the ice sheet, and subsequently upon the disposition of glacial and post-glacial deposits laid down at the retreat of the ice. The main features of these events, so far as they are known, will be brought out in the following discussion of Pleistocene history.

PLEISTOCENE AND POST-PLEISTOCENE GEOLOGY

Although brief notes on the Pleistocene deposits of the Athabaska–Great Slave Lake region are to be found in nearly all the survey reports that have been published, attempts to fit the material into a consistent Glacial and post-Glacial history are rare. The most satisfactory to date is in a short

paper by A. E. Cameron (1922–A) on post-Glacial lakes in the Mackenzie basin. In most of the discussion that follows I shall draw freely upon this paper, using also interpretations that I have made in connection with earlier work (1930–A, B, 1935).
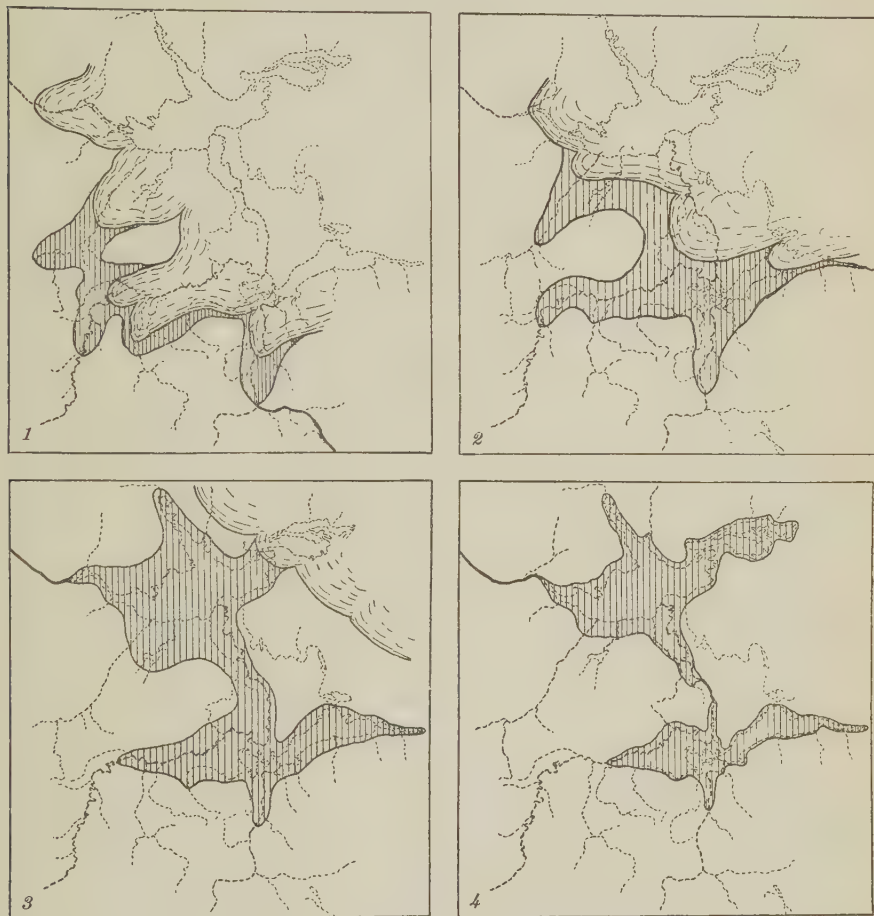

FIG. 3. Post-Glacial lake expansions in the Athabaska–Great Slave Lake region when the water, impounded against the front of the Keewatin ice sheet, stood at about the 1600-foot level (1), the 1100-foot level (2), the 800-foot level (3), and the 700-foot level (4). (Reproduced by permission of A. E. Cameron.)

The dating of the last advance and retreat of ice in this region is still problematical. According to earlier concepts, centers of glacial activity moved progressively from west to east around Hudson Bay (Tyrrell, 1898), so that the surface in our region would be older than those in Labrador and Quebec. In recent years, however, Antevs (1934, 1936, 1938) has proposed that the final event of the last, or Wisconsin,

glaciation was a rejuvenation of the Keewatin and Cordilleran glaciers. Flint (1943) maintains, further, that the evidence from striae, upon which the old idea of a progression of centers was based, can be applied only to the late stages of glacial activity. He believes that there was a single continental ice mass on the occasion of each advance and retreat. In the event that either Antevs or Flint is correct, the land surfaces in our region, instead of being old in terms of post-Glacial time, would be among the youngest. As will be shown below, there is some biological evidence in support of this concept.

The Keewatin glacier is thought to have come into this region from the northeast, following drainage lines that had long been established in the Laurentian Plateau. These lines probably occupied depressions that now, much deepened, hold Athabaska and Great Slave Lakes (See Alcock, 1920, for a discussion of the origin of Lake Athabaska). The ice crossed the valley now occupied by Slave River and sent tongues into the Cretaceous uplands by way of the ancient valleys that had been carved out of them. The outlying Cretaceous plateaus are thought to have been sufficiently high and resistant to determine the direction of movement of the ice and to divide it into lobes. According to Cameron, "At least three definite glacial lobes are apparent in the area. One extending up the valley of Hay River; a second swung west, south of the Caribou Mountains, and probably sent tongues up the valleys of the Peace and Wabiskaw rivers; while a third lay in the basin of Athabaska lake with its tongue pointing up the valley of Athabaska river."

A correlation of this ice advance with one of the three now commonly recognized for Wisconsin time (Iowan, Tazewell-Carey, Mankato) has not been definitely established. Rutherford (1941) and Bretz (1943) have outlined the terminal Late Wisconsin moraine in central Alberta and southern Saskatchewan. This is called the Altamont or Coteau, and is correlated with the Des Moines, Mankato, and Port Huron moraines farther to the southeast. It enters Canada at the Montana–North Dakota boundary, and extends northwestward in a slightly arcuate pattern so as to cross the North Saskatchewan River about 75 miles east of Edmonton, Alberta. Halliday and Brown (1943) have drawn a provisional connection between a southern portion of this moraine in Saskatchewan and the lobate ice front proposed by Cameron in the Athabaska–Great Slave Lake region. They have carried the hypothetical moraine northward entirely within the province of Saskatchewan, whereas, according to Rutherford and Bretz, it should continue northwestward into Alberta nearly to lat. 55°, northeast of Edmonton. If the latter is the case the extreme limits of the Late Wisconsin (W_3) glacial lobes in the southwestern part of the Mackenzie basin probably were farther up the Athabaska and Peace Rivers than Cameron placed them as dams for his 1600-foot lake (see below). In fact there is no evidence in Cameron's paper (1922–A) that he considered these to be terminal lobes. In any event it seems reasonable to look upon the lake stages and moraines in the Athabaska–Great Slave

Lake region as representing recessional stages of the Late Wisconsin (Man-
kato) ice, approximately equivalent to similar stages noted in Manitoba
and Ontario.

As the fronts of the lobes receded, the waters from the upper basins
of the Hay, Peace, and Athabaska Rivers were impounded against them to
form large post-Glacial lakes. *Figure 3*, reproduced from Cameron's
paper, will show the approximate boundaries of the lakes and ice lobes
at the four stages. From studies of terraces in the valleys of the
main rivers, elevated shore lines on the great lakes, and from the results
of meridional and base-line surveys and the distribution of moraines,
Cameron has designated four of these ancient lakes, formed successively
at levels which are now about 1600 feet, 1100 feet, 800 feet, and 700 feet
above the sea. Outlets for at least the earlier of these lakes were probably
toward Hudson Bay, since the normal route to the Mackenzie valley would
have been blocked by ice.

The lowest of the lake stages is at approximately the same level as
modern Lake Athabaska (699 feet). It will be noted that at this time
there were probably long extensions of this lake southward into the lower
Athabaska valley, westward up the Peace, and northward down the Slave.
Great Slave Lake was somewhat larger than it is now, with a long southern
arm that probably reached to the present site of Fort Smith. The lake
may have been somewhat lower than Lake Athabaska then, as it is now
(495 feet). The Athabaska and Peace Rivers are huge streams, rising
in the Rocky Mountains and bearing heavy loads of debris. In the interval
since the drainage of the 800-foot lake they have filled the southern,
western, and northern arms of Lake Athabaska with alluvium, and have
completely eliminated the southern arm of Great Slave Lake. In doing
so they have formed most of the Mackenzie Lowland physiographic
province in our region (for further discussion of these great alluvial
deposits see Kindle, 1918).

From the above notes it will be seen at once that most of the soils and
surfaces in the Mackenzie Lowland and Alberta Plateau Provinces, as well
as those on the slopes if not the summits of the Cretaceous plateaus,
acquired their modern form as a result of late Glacial and post-Glacial
events. From southwest to northeast on the Alberta Plateau there are
at least four recognizable surfaces that are progressively younger in that
direction. They are covered by fine-textured lacustrine soils interspersed
with morainic ridges and outwash laid down as the successive ice fronts
receded. Above the four is the still older surface on the tops of the
Cretaceous plateaus. The botanical significance of these surfaces in the
Wood Buffalo Park has already been discussed at some length (Raup,
1935) and will not be duplicated here. Studies similar to those on the
Wood Buffalo Park should be made in the country around the western
arm of Great Slave Lake, particularly in the tract bounded on the east
by the north and west arms and on the west by the Horn Mountain plateau.

The phytogeographic importance of Pleistocene erosion and deposit in

the Laurentian province is fully as great as over the Paleozoic and younger rocks, but in quite different terms. The complete removal of residual or earlier morainic soils from most of the surface, without any large or continuous deposits by the ice as it receded, has given the region much of its sterile aspect. The excavation of countless small and large depressions, the disruption of old drainage patterns, and the removal of the fine materials which, carried by streams, could act as eroding agents, have served to accentuate the sterile condition and to retard for a long period the development of integrated drainage systems. At the same time there has been a phenomenal development of lake and pond shore vegetation, resulting in wide expanses of muskeg and swamp.

Of great interest in the problem of vegetational development are time and space relations analogous to those west of the pre-Cambrian boundary. The present shores of Athabaska and Great Slave Lakes are subtended by complex systems of ancient shore lines reaching hundreds of feet above the present lake levels. At Charlot Point on the north shore of Lake Athabaska I have measured them up to about 200 feet, and Stockwell (1932) has found them 540 feet above the eastern end of Great Slave Lake (See also Blanchet, 1926). Not only has the fall in water levels made possible a series of successional stages in the development of vegetation on the main lake shores, but it also caused a time sequence in the development of upland pond and ridge vegetation.

If Cameron's disposition of the ice lobes at his various lake stages is correct, then approximately the western half of Lake Athabaska and large areas of the Laurentian plateau north and south of it were under the 1100-foot lake. At the same time Great Slave Lake and most of the Laurentian Plateau north of Lake Athabaska were still under ice, while a vast area of the Athabaska sandstones south of the 1100-foot lake was exposed. Except for the last, therefore, no part of the Laurentian Plateau in our area was finally exposed for the development of its modern vegetation until after the drainage of the 1100-foot lake and the next retreatal stage of the ice. Even then, according to Cameron, the McLeod and Christie Bay areas of Great Slave Lake were still under the ice. It is presumed that when the lake reached its 800-foot stage most of the Tazin and Taltson and upper Thelon basins between Athabaska and Great Slave Lakes were exposed. This would make their present surfaces of about the same age as the Alberta Plateau in the western part of our area. Pre-Cambrian areas just east of the north arm of Great Slave Lake would be of about the same age, but the exposure of the region around McLeod and Christie Bays, as well as the Lockhart basin, would date from the drainage of the 800-foot lake and the further retreat of the ice front, and so would not be much older than the alluvial deposits of the lower Athabaska, Peace, and Slave Rivers. There is an apparent inconsistency in the high ancient shore-lines at the eastern end of Great Slave Lake, for they extend far above 100 feet. This, however, is considered due to differential uplift following the retreat of the ice to the northeastward (See R. Bell, 1900:
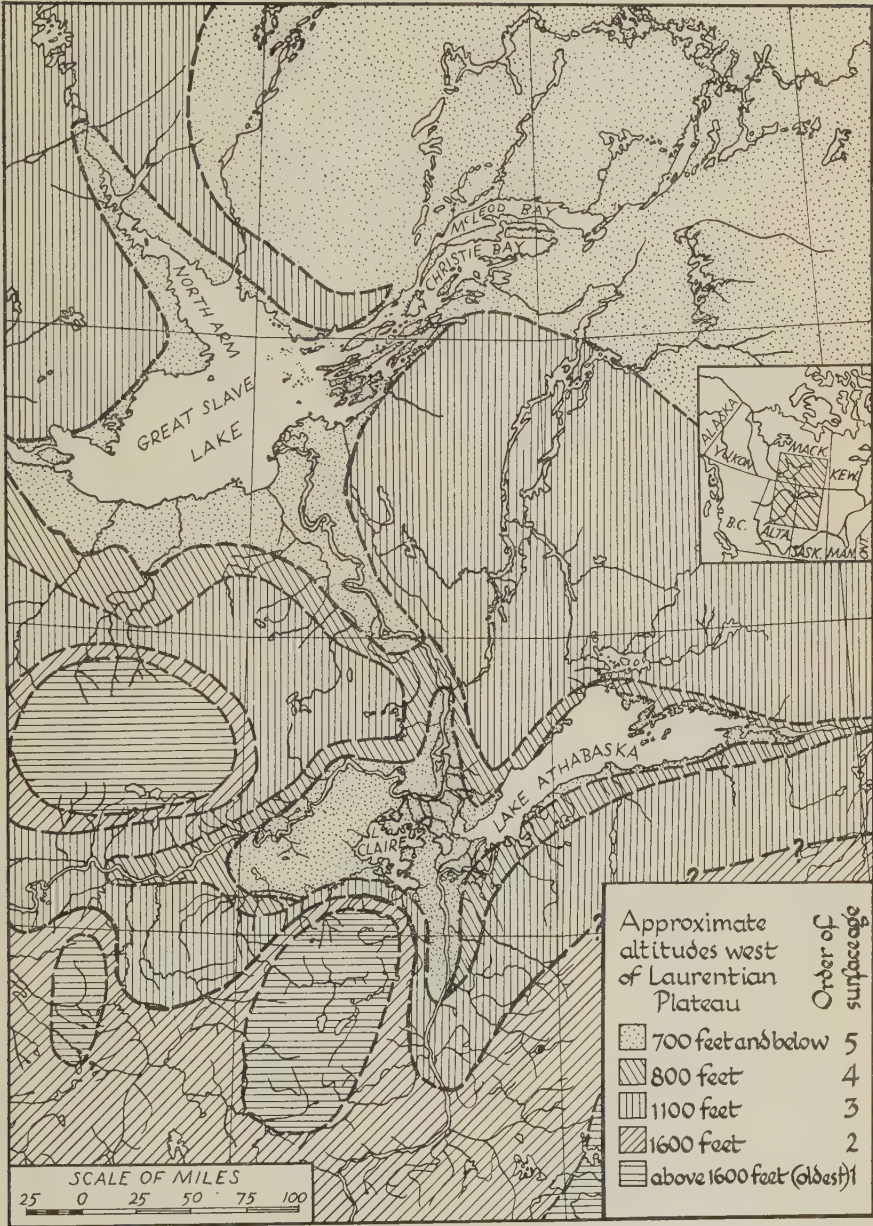
Fig. 4. Map showing the relative ages of land surfaces in the Athabaska–Great Slave Lake region, with approximate altitudes in the area west of the Laurentian Plateau.

Cameron, 1922–A, B; and Raup, 1930–A, for discussion of ancient shore lines at Great Slave Lake). If such an uplift has occurred since the drainage of the 800-foot lake and the recession of the ice from McLeod and Christie Bays, then the surfaces immediately around these Bays, and possibly also parts of the Lockhart basin, are still younger than the Mackenzie Lowland alluvium.

Following the hypothesis just outlined, therefore, the oldest surface in the Laurentian Plateau is probably somewhere in the upland country south of Lake Athabaska. It would correspond in age possibly to the bottom of the 1600-foot lake. Next would come the area between and around the two great lakes except for the eastern part of Great Slave Lake and the Lockhart basin. It would correspond in age to the Alberta Plateau surface. Third would be the strip of country, comparatively narrow, around Lake Athabaska. It would be of about the same age as the bottom of the 800-foot lake which is now occupied by the "Salt Plain" southwest of Fort Smith, and which has extensions in the lower Peace and Athabaska valleys as well as below the Alberta Plateau escarpment south of Great Slave Lake. Fourth in age are the uplands around McLeod and Christie Bays and the Lockhart basin, which would be of about the same age as the Mackenzie Lowland; and finally there would be the most recent surfaces, exposed around the eastern arm of Great Slave Lake by differential uplift. Some vegetational evidence for such a sequence will be found in subsequent discussions, but more exploration is necessary before conclusions can be reached. This is especially true for the country between the Clearwater River and Lake Athabaska, and between the latter and Great Slave Lake. *Figure 4* is a map on which I have attempted to show areas of approximately equal age. Some light eventually may be thrown upon the more recent changes of water levels in Great Slave Lake by a study of the extensive peat deposits which occur near the head of the Mackenzie River. Some of the islands at the western end of the lake appear to be composed entirely of peat, remnants of an ancient muskeg area that has been for the most part eroded away in old river channels or by wave action.

<div align="center">CLIMATE</div>

An adequate description of the climates of the Athabaska–Great Slave Lake region is at present beset by well-nigh insurmountable difficulties. Most of the published meteorological data, like those on other natural phenomena, have come from the older fur-trade settlements along the main routes of travel. Observations in the Laurentian Plateau, therefore, are exceedingly scanty, and for most of that area there are only miscellaneous notes made by travelers. Observations made in connection with air navigation have not yet become available, but it is hoped that they will greatly enlarge our knowledge of the climate of the whole region. Even if we had adequate meteorological observations, there would still be difficult problems of interpretation. The relation, for instance, between summer precipitation and soil moisture, expressed in terms of its significance

to plant growth, is complicated by soil-frost phenomena and low air temperatures. Evaporation data, now non-existent, will be needed before these problems can be attacked. Furthermore, this appears to be a region of steep micro-climatic gradients which need to be recorded and analyzed before the climate of the area as a whole can be understood.

In general the region has a northern continental climate, with long cold winters, short comparatively warm summers, and low annual precipitation. It is further distinguished from more southern districts by its long summer days (See Koeppe, 1931, pp. 1–5).

TEMPERATURE

Table of Temperatures (degrees F.) Averaged over a Period of Ten Years, 1917–1926

		Chipewyan	Fort Smith	Resolution	Hay River
Monthly mean minimum	Jan.	−19.6	−24.0	−22.4[1]	−22.4
	July	51.1	46.7	51.2	50.0
Absolute minimum	Jan.	−49.0	−53.9	−47.9[1]	−49.4
	July	35.3	33.3	40.0	38.4
Monthly mean maximum	Jan.	− 2.1	− 7.5	− 8.6[1]	− 4.3[2]
	July	72.8	72.8	68.6	68.1
Absolute maximum	Jan.	26.2	19.2	15.5[1]	25.1[2]
	July	86.4	88.1	83.4	86.8

[1] Averaged over seven years (1920–26) due to lack of records.
[2] Averaged over nine years, records for 1918 being absent.

Of particular significance to the growth of plants are the lengths of summer frost-free periods, the rates of seasonal progression, and the incidence of soil frost. Very few data have been compiled on the average lengths of frostless seasons. To be truly significant, such data should be gathered in specific areas over periods of years, with observations not confined to actual minimum temperatures but including local effects upon growing plants. In the absence of such information we must be content with minimum temperature data recorded at weather stations; and we must use them with the understanding that microclimatic variations in local situations around the various stations may be so great that the data do not present average local conditions. Albright's findings at Beaverlodge, in the upper Peace River region (1933), will serve to illustrate this point, and probably could be duplicated in many places throughout our area. He found that the length of the frost-free season on the top of a hill 134 feet high was about 96.7 days (averaged over a three-year period), while in a slough at the foot of the hill it was only 29.3 days.

Average frost-free periods have been computed from absolute minimum temperatures of 32° F. or below for McMurray, Fort Chipewyan, and Vermilion. The averages are from records for nine years at McMurray and Chipewyan, and for eight years at Vermilion (Raup, 1934). Mc-Murray shows an average frostless season of about 65 days, Fort

Chipewyan 72 days, and Vermilion 79 days. The amount of variation in the length of the seasons during the same period is perhaps of greater significance than the average. At McMurray the longest was 101 days and the shortest only 29 days. Corresponding figures for Chipewyan are 106 days and 58 days, and for Vermilion 104 and 48 days. Further evidence that the growing season is apt to be short or interrupted comes from data gathered over longer periods. July can be regarded as the warmest month of the summer, yet minimum temperatures of 32° F. or lower were recorded in July at Chipewyan nine times in the forty-five years between 1884 and 1928, five times at Vermilion between 1905 and 1928, and six times at Fort Smith between 1913 and 1928. Such low temperatures are much more common in June and August. In forty-five years' records at Chipewyan they were recorded twenty-eight times in June and twenty-four times in August. At Resolution, where July minima of 32° did not occur at all between 1914 and 1928, the June minima fell to 32° or below thirteen times, and the August minima twice. Even from these scanty figures it is clear that the summer frostless season is short and extremely hazardous. It centers in July, but over most of our region frost may occur even in this month.

The above data suggest that the large lakes have an ameliorating influence upon temperatures in their immediate surroundings. The monthly mean and absolute minimum and maximum temperatures for January and July given in the table indicate that in winter lower temperatures are experienced at Fort Smith and Vermilion than at settlements on the lakes, and cool periods in summer reach lower temperatures inland than on the lakes. It has already been noted that Resolution shows no July minima as low as 32° for the period studied, while Hay River shows only one in the long period between 1893 and 1928. Next to the Great Slave Lake stations is Chipewyan, but this is at the narrow western end of Lake Athabaska where the water is shallow.

The opening of spring near the lakes is conditioned to a considerable extent by the dates at which the lake ice finally disappears. The effects are seen in the figures for June and August minima. The ice usually leaves Lake Athabaska during the first half of May, but it commonly remains in Great Slave Lake until late June. Minima of 32° or below occurred at Chipewyan about an equal number of times in June and August, while at Resolution they occurred thirteen times in fifteen years during June, and only twice in August. At Great Slave Lake, therefore, the frost-free season is not only longer, but comes later in the season.

The dates of opening and closing of rivers and lakes have been recorded for many years in the north, for they set the time limits of summer travel. The lower reaches of the Athabaska and Peace Rivers usually open about the first of May, but the western part of Lake Athabaska is not free of ice until about May 10th. Floes of ice blown to and fro by the wind may remain in the lake until mid-June. In the fall the shallow western end commonly freezes over about mid-October, but at Fond du Lac not until about the middle of November. Some of the wider and deeper parts of the

lake are open until well into December (Alcock, 1936). There is con-
siderable variation in these dates from year to year, as pointed out by
Kindle (1920).

Blanchet (1926) gives the following dates for the disruption and setting
of ice at several places on Great Slave Lake: Resolution, June 1 to 20,
October 15 to November 15; Rae, May 25 to June 15, October 5 to 25;
Old Fort Reliance, June 25 to July 5, October 1 to 20. The upper
Mackenzie River usually opens between May 5 and May 20, and sets
again in the latter half of November. Lakes in the Lockhart basin are
commonly not completely free of ice until late July, and set again in
October or late September (Clarke, 1940).

The vegetation in the Wood Buffalo Park usually has its spring aspect
well developed during the first week of June. At that time the early
Pulsatilla ludoviciana is rather past the height of its flowering and *Calypso
borealis* is in its best development. The upland areas, away from the main
rivers, are apt to be several days later in the growth of their spring flora
than the lowlands. The autumn is usually reckoned to begin about mid-
August, and frosts are likely to be frequent after that date. The fall
flora, typified by the goldenrods and asters, and by the ripening of the
fruits of raspberries, dogwoods, roses, mooseberries, and blueberries, is
well advanced by the third week in August. Throughout the season there
is a notable "telescoping" of the seasonal aspects of the flora. *Calypso*
has been found in flower as late as June 26, and goldenrods as early as
July 19.

One of the most significant effects of the subarctic climate, biologically
speaking, is soil frost. A permanently frozen condition in some kinds of
subsoil, and the comparatively short season during which the surface
layers are thawed, greatly influence the distribution of plants by limiting
root development, maintaining high water tables, affecting the nature of
the drainage, slowing down the processes of humus formation and the
maturation of soils, and by allowing only a short period in the year for
erosion and deposit. There are also the effects of solifluction upon the
development of vegetation, now and in the past. Very few data have been
gathered with which to attack any of these problems in our region, so
that the whole field remains to be investigated.

Solidly frozen ground was found at a depth of about five feet on a cleared
bank of the Slave River early in August, and at 37 inches in an open
prairie near the base of the Caribou Mountain Plateau on June 26. It
was found one foot beneath the surface on an exposed sunny hillside
high in the Caribou Mountains on July 12. On the other hand a pit six
feet deep in a sand plain on the north shore of Lake Athabaska in July
showed no frost at all. Lefroy (1886) reported the ground thawed to
about 4 feet in summer at Fort Rae, and to eleven feet at Fort Simpson on
the Mackenzie. Preble (1908) states that "In excavating a cellar on a
sandy ridge in the midst of a field [at Fort Simpson] on July 21, 1903,
frozen ground was reached at a depth of seven feet. In October, 1903,
an excavation made in the yard of a dwelling house revealed frozen ground

at seven feet." Richardson (1851) reported a thawed layer ten feet seven inches deep in "a heavy mixture of sand and clay" at Simpson in 1836. McConnell states that "Around Great Slave Lake the soil seldom thaws out to a greater depth than eight feet, and in many of the muskegs and marshes ice remains throughout the year at a depth of about two feet." Richardson (1828) says that the soil at Fort Franklin, on Great Bear Lake, did not thaw deeper than 21 inches in the summers of 1825 and 1826.

The permanently frozen subsoil tends to lessen the amount of seepage and to increase the run-off. In poorly drained areas it encourages the widespread development of muskegs, with their typical vegetation of plants suitable to acid soils. The low temperatures and acid conditions render very slow the successive movements in the development of vegetation which are dependent upon chemical and physical changes in the soil. Such movements, also, which follow topographic change and the formation of new barren areas for colonization by plants, are greatly retarded by the shortness of the season available for erosion and deposit. These retarding influences are especially significant in a study of the probably young vegetations just beginning their development upon land surfaces recently exposed in the Athabaska–Great Slave Lake region.

The effects of frost as a soil-forming and soil-disturbing agency are not readily seen in most parts of this region, though they must have had a large influence upon the early stages of the vegetation. How great this influence was, and how long it lasted, are as yet unknown. Newly formed soils on the limestone hills in the Laurentian region have undoubtedly been derived from rocks disintegrated at least in part by frost action.

As will be shown in another part of this paper, there seems to be a relationship between the ranges of certain trees and the depth to which the ground thaws during the growing season. Sandy soils that thaw deeply will support plants that require a deep tap root, while heavier soils and muskegs in which frost remains near the surface throughout the year preclude the growth of such plants.

PRECIPITATION

Total precipitation for the year in the western part of our region (rain plus snow reduced to a water equivalent) probably averages between ten and fifteen inches (Koeppe, 1931, p. 109). Alcock estimates that it is about thirteen inches around Lake Athabaska, and Koeppe (ibid.) gives average totals of twelve or thirteen inches for Chipewyan and Vermilion. According to Connor (1938) it is about 11.3 inches at Hay River. A considerable part of this is in the form of snow. Yearly snowfalls, averaged over ten years (1917–1926), are as follows: Chipewyan, 53.3 inches; Vermilion, 34.3 inches; Fort Smith, 37.3 inches; Hay River, 45.4 inches; Resolution, 50.6 inches.

Rainfall during the months of June, July, and August is probably the most important element in the precipitation so far as plants are concerned. Soil moisture in spring is abundant due to melting snow; but in summer the lighter upland soils become droughty, and rain must supply the needed

moisture. Heavier soils, having a higher permanent frost line, commonly remain moist throughout the year in spite of very low summer precipitation. The following statement shows some average rainfall totals for June, July, and August.

Average in inches: McMurray, 7.08; Chipewyan, 5.3 (43 yrs.); Fond du Lac, 5.29 (8 yrs.); Vermilion, 6.05 (22 yrs.); Fort Smith, 5.36 (9 yrs.); Resolution, 4.11 (10 yrs.); Hay River, 4.9 (10 yrs.).

From these few figures it is clear that summer rainfall is extremely low throughout our region. It seems to be greatest at "inland" stations, away from the shores of the main lakes, and progressively lower from south to north. No data are available for the eastern end of Great Slave Lake, but it is to be presumed that the rainfall decreases in that direction also. It is about 3 inches at Coppermine on the Arctic coast, and about 4.7 inches at Simpson (see Connor, 1938). By way of contrast, rainfall in June, July, and August at Edmonton in central Alberta totals about 9 inches. A more reasonable comparison is possible if a longer growing season is allowed for the Edmonton area, including May and September and making a total summer rainfall of about 12 inches.

It may be said, therefore, on the basis of the scanty climatic data at hand, that the climate of our region "deteriorates" from south to north, or more probably from southwest to northeast. Summer rainfall decreases in that direction, and the open seasons are progressively shorter. The large bodies of water tend to ameliorate temperatures in their vicinity, and at the same time tend to make the open season somewhat later in the northern districts than farther south.

TYPES OF VEGETATION IN THE ATHABASKA–GREAT SLAVE LAKE REGION

Types of vegetation in the Athabaska–Great Slave Lake region fall naturally into five categories: forest, marsh or muskeg (including various shore line communities), grassland, lichen-heath communities, and dune scrub. The following is an outline of types to be treated in this and ensuing papers (see map, *Fig. 5*).

> 1. Forests
>   White spruce
>   Park-like white spruce
>   Flood plain spruce
>   Upland mesophytic spruce
>   Jack pine
>   Balsam fir–white spruce
>   Black spruce–lodgepole pine
>   Bog forests
> 2. Shore and muskeg vegetation
>   In ponds and small lakes
>   On the shores of larger lakes
>   River flood plain and delta communities
> 3. Grassland
> 4. Lichen-heath
> 5. Dune scrub

The forest is predominantly coniferous, and it is bounded at the northeast by arctic tundra which appears in the Lockhart basin. Marsh and muskeg are of wide occurrence over the entire area, due not only to the immature condition of drainage systems, but also to the presence of a permanently frozen subsoil which keeps the water-table relatively high. There is a concentration of grass and sedge marsh in the deltas of the great rivers, such as the Peace, Athabaska, and Slave, while muskegs are more extensively developed on the uplands. Grasslands are mainly confined to the gently sloping lacustrine soils of the country west of the Slave River, but counterparts of them have been described in the region northwest of Great Slave Lake and in the Liard River country. Modified grasslands have also been found associated with certain soils on the north shore of Lake Athabaska. Lichen-heath covers vast areas of rock outcrop and sand plain. It is one of the most characteristic vegetation forms of the entire region, varying from associations of crustose lichens, interspersed with a few mosses, to thick masses of fruticose species with or without mats of trailing heaths or heath-like plants. Dune scrub occurs on the larger sandy beaches, but it is best developed on the great shifting dunes which are found south of Lake Athabaska.

Most of the more mesophytic forests surrounding Athabaska and Great Slave Lakes are of white spruce (*Picea glauca*) and jack pine (*Pinus Banksiana*). The relations between these will be discussed in more detail in another place, but some further notes on the divisions of the white spruce forests are in order. These occur in three phases which are geographically rather distinct. On the river flood plains of the Athabaska, Peace, and Slave Rivers the trees grow to large size (75–100 feet high and 2–3 feet in diameter), and in close, nearly pure stands. The undergrowth is relatively thick, but the ground flora is sparse, with a relatively thin carpet of mosses. Closely related to this type is that of the better-drained soils on the uplands. Here the stands are not quite so dense, and the undergrowth is thinner. The ground is covered, however, with a mat of mosses and duff 4–10 inches thick. The trees themselves are often larger than those of the flood plains. The third phase of the spruce forests is quite different, consisting of open park-like stands with practically no undergrowth. The ground is usually covered with a lichen-heath mat, and the soils are usually light and sandy. This type is best developed in the northeastern part of the lake region, but representatives of it are occasionally met with in the regions west of the Slave River and about Lake Athabaska.

Muskeg forest throughout the region is distinguished by black spruce (*Picea mariana*) and larch (*Larix laricina*). The former is by far the more abundant and often forms thick, nearly pure stands.

Two other types of forest, not widely spread in our area, are those of balsam fir (*Abies balsamea*) and white spruce, and those of lodgepole pine (*Pinus contorta* var. *latifolia*) and black spruce. These occupy, respectively, the flood plains of the lower Athabaska and Clearwater Rivers, and the higher slopes of the Caribou Mountains.

The semi-open prairie or parkland vegetation of the Wood Buffalo Park is characterized by abundant stands of trembling aspen (*Populus tremuloides*) which are locally known as "poplar bluffs," and which margin and subdivide the grassland areas. Whether these are stable types of forest is uncertain, since the aspen most commonly follows fire on the lighter upland soils in this region. Also, some prairies which are margined by white spruce have been described at the base of the Caribou Mountains (Raup, 1935). The prairies themselves occur in several phases, ranging from xerophytic types on dry south-facing bluffs to wet types on poorly drained uplands.

Shore vegetation is extremely variable throughout the region, but it can be subdivided roughly, for purposes of description, into the communities of ponds and small lakes, those on the shores of larger bodies of water such as Athabaska and Great Slave Lakes, and those of local river deposits and delta plains.

FORESTS

PARK-LIKE WHITE SPRUCE FORESTS

GREAT SLAVE LAKE

The park-like spruce forest which grows about the eastern arm of Great Slave Lake may be divided into four phases which intergrade freely. They are developed most extensively on the ancient lake beaches and sand plains that abound in this district, and the variations in the content, density, and relative mesophytism of their flora are determined largely by the nature of the substratum. The most xerophytic type inhabits stony beach ridges whose water-holding capacity is extremely low. Such ridges contain almost no fine materials. Somewhat more mesophytic is the sand plain type which is the commonest association at Old Fort Reliance. Between this and the stony ridges in degree of mesophytism are old beaches formed of small flat pebbles weathered out of slates which occur near the tip of Fairchild Point (see Stockwell, 1933). These pebbles disintegrate rapidly under the influence of wave action and subsequent weathering to form a clayey admixture to the otherwise very permeable soils. At the other end of the scale of mesophytism are the rocky hills with their crevice floras. In some places, particularly on the metamorphosed sedimentary rocks of Fairchild Point, considerable residual soil has accumulated and supports an open but relatively rich forest of spruce. Some of the higher sand plains whose timber has not recently been disturbed by fire have also developed a considerable humus layer which also supports rather rich woods.

The trees in the park-like spruce forest are widely spaced and branched all the way to the ground. There is little or no shrubbery, but the soil is frequently covered with a dense growth of bunch lichens and mat-forming shrubs. The following list is typical of the timber which is common on sand plains.

PRIMARY SPP.: *Picea glauca,*[1] *Betula papyrifera* var. *neoalaskana, Cladonia rangiferina, Cladonia alpestris, Cetraria islandica.*

SECONDARY SPP.: *Juniperus communis* var. *montana,*[2] *Calamagrostis purpurascens, Salix Bebbiana, Betula occidentalis,*[3] *Pulsatilla ludoviciana, Saxifraga tricuspidata, Geocaulon lividum, Empetrum nigrum, Epilobium angustifolium, Arctostaphylos Uva-ursi, Vaccinium uliginosum, Vaccinium Vitis-Idaea* var. *minus, Pedicularis labradorica, Solidago multiradiata.*

Empetrum and *Arctostaphylos Uva-ursi* are the commonest mat plants.

On sandy ridges, particularly those exposed to storm winds, the surface of the soil is likely to be partially barren of vegetation, and the habitat in general much drier. Here the trees are farther apart, and *Empetrum nigrum* becomes a primary member of the ground flora, acting as a sand-binding agent. Another species which must be considered of first importance on the ground is the psammophilous lichen *Stereocaulon paschale.* It covers extensive areas, and its thallus is fairly impregnated with drifting sand. The secondary species are much the same as those noted above, but they occur in smaller numbers. *Poa glauca, Artemisia borealis,* and *Oxytropis splendens* appear occasionally to represent the more xerophytic habitats of the dry sand beach ridges.

Where the spruce woods grow on stony plains and beach ridges, the more xerophytic phase, to be found usually near the lake shore, contains a group of species suggestive of rock crevices or shingle beaches. The surface of the ground is fairly well covered in the depressions between the ridges by lichens (*Cladonia* spp., *Cetraria* sp.) and a mat of *Dryas.* Both *Dryas integrifolia* and *D. Drummondii* function in this manner, but the first is more abundant. *Arctostaphylos Uva-ursi* forms a few mats, and *Calamagrostis purpurascens* is one of the more common herbs. The following list will indicate the general structure of this flora (see also *Plate* 1).

PRIMARY SPP.: *Picea glauca, Cladonia* spp., *Cetraria* sp., *Dryas integrifolia.*

SECONDARY SPP.: *Juniperus communis* var. *montana, Calamagrostis purpurascens, Saxifraga tricuspidata, Dryas Drummondii, Potentilla nivea* var. *subquinata, Hedysarum alpinum* var. *americanum, Oxytropis viscidula, Shepherdia canadensis, Arctostaphylos Uva-ursi, Erigeron compositus* var. *trifidus, Solidago multiradiata.*

At slightly higher levels, farther away from the lake shores, this rather simple and open association gives way to a much denser one which resembles the drier sand plain flora described above. The ground is covered on both ridge and depression surfaces. *Arctostaphylos Uva-ursi* increases in prominence as a mat plant at the expense of *Dryas,* and the bunch lichens cover relatively more surface. A few species are added

[1] In this and the following discussions of forest types *Picea glauca* is considered in its broad sense, as it was in the published Catalogue. It should be understood, however, that our region appears to contain both the typical eastern form and the western var. *albertiana,* inseparably mixed in most cases but possibly segregated in others. For a discussion of these forms and their distribution see p. 73.

[2] *Juniperus communis* var. *saxatilis* of some recent authors, non Pall.

[3] *Betula microphylla* of the Catalogue. See Rhod. 47: 313–317. 1945.

to the list of secondary ones: *Geocaulon lividum, Arctostaphylos rubra, Empetrum nigrum, Arnica lonchophylla,*[4] and *Habenaria obtusata.*

A more mesophytic forest, closely resembling that of the higher sand beaches and plains described above, develops on the higher stony ridges. There is a thick carpet of woodland mosses with a rich growth of *Empetrum nigrum, Arctostaphylos rubra, Peltigera canina,* and *Vaccinium Vitis-Idaea* var. *minus.* Patches of *Vaccinium uliginosum* appear, and *Pedicularis labradorica* is common. In places a distinct low shrub layer is formed of *Vaccinium uliginosum, Ledum groenlandicum, Ledum palustre* var. *decumbens,* and *Alnus crispa.* With the increase in mesophytism a number of additions are made to the occasional flora of the association:

> *Equisetum scirpoides, Equisetum pratense, Tofieldia palustris, Cypripedium passerinum, Calypso bulbosa, Arenaria lateriflora, Aquilegia brevistyla, Rosa acicularis, Pyrola secunda, Pyrola virens,*[5] *Pyrola asarifolia* var. *incarnata, Gentiana Amarella, Linnaea borealis* var. *americana, Senecio cymbalarioides* var. *borealis.*

To summarize, the park-like spruce forest on beaches and sand plains of Great Slave Lake may be described as an open stand of *Picea glauca* with or without an admixture of *Betula papyrifera* var. *neoalaskana.* The latter is commonest on sand, while the pure spruce is usually on stony soils. In its most mesophytic phase the timber has a thick mat of woodland mosses and lichens and a low shrub layer in which *Vaccinium uliginosum, Vaccinium Vitis-Idaea, Empetrum nigrum, Ledum groenlandicum, Ledum palustre* var. *decumbens, Betula occidentalis,* and *Arctostaphylos rubra* are prominent. More xerophytic phases, whether on sand or shingle, have the trees more widely spaced, the mosses largely replaced by bunch lichens, and the shrub layer reduced to mat-forming plants such as *Empetrum nigrum, Arctostaphylos Uva-ursi, Dryas integrifolia,* and occasional bushes of *Juniperus communis* var. *montana* or *Betula occidentalis.* *Empetrum* and *Arctostaphylos Uva-ursi* are characteristic of sandy substrata, and *Dryas integrifolia* of stony surfaces. Secondary species are drawn from xerophytic rock crevice associations, all of which will be described further in another paper.

The most mesophytic forest seen by the writer on the eastern arm of Great Slave Lake closely resembles that described above. It occurs on those parts of the rocky hills of Fairchild Point which are not exposed to excessive storm winds, and which have the softer metamorphosed sediments as substrata. Here a thin residual soil has developed in post-Glacial time; and the subsurface drainage, due to the dip of the strata and the presence of soil, has been sufficient to prevent the development of true muskeg. *Viburnum edule,*[6] a characteristic species in rich woods about Lake Athabaska and in the great river lowlands, appears in this upland forest though it is otherwise rare at the eastern extremity of Great Slave Lake. Like other mesophytic spruce forests of our region, this one

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[4] *Arnica chionopappa* of the Catalogue. See Brittonia 4: 428–30. 1943.

[5] *Pyrola chlorantha* of the Catalogue. See Rhod. 43: 167. 1941.

[6] *Viburnum pauciflorum* of the Catalogue. See Rhod. 43: 481–483. 1941.

is exceedingly poor in species. It has two phases which are freely inter-mingled, and which appear to be due to alternating crevice and low ridge areas.

PRIMARY SPP.: *Picea glauca.* Ridges: *Arctostaphylos Uva-ursi, Linnaea borealis* var. *americana, Cladonia alpestris* and woodland mosses. Depressions: *Ledum groenlandicum, Vaccinium uliginosum,* woodland mosses.

SECONDARY SPP.: Ridges: *Calamagrostis purpurascens, Geocaulon lividum, Dryas integrifolia, Rosa acicularis, Epilobium angustifolium, Arnica lonchophylla, Senecio cymbalarioides* var. *borealis.* Depressions: *Empetrum nigrum, Vaccinium Vitis-Idaea* var. *minus, Arctostaphylos rubra, Viburnum edule.*

It will be noted that the ridge, or drier phase of this forest forms a transition to that of the sandy and stony surfaces described above. Also, it is obvious that the more mesophytic phases of the latter are almost identical with the depression phase on the rock hills.

Granite hills in the vicinity have a much poorer forest flora. It is limited to crevices and small glacial deposits, and most of the rock surface bears only lichens and occasional mosses. There is almost no residual soil such as appears on the old sediments, and depressions of any kind are likely to be entirely undrained. Muskegs, therefore, are much more extensively developed. Where an open forest does occur, moreover, it has more white birch in it than grows on the residual soils.

LAKE ATHABASKA

Park-like forests of white spruce are common on the shores of Lake Athabaska. Unlike those at the eastern end of Great Slave Lake, however, they do not usually spread over a broad series of ancient beaches and sand plains, but are confined to one or two ridges immediately above the present shore-line (*Plate 1*). Only two exceptions to this have thus far been observed: one on the conglomerates and dolomites of the north shore of the lake, and the other in certain sand dune habitats near the south shore. As a general rule one has only to pass over those ridges which occur just above the shore to be through the belt of spruce and into the jack pine. The actual elevation of the ridges above the level of the lake seems not to affect this arrangement in the least. Comparatively low, gently sloping sand beaches just west of Ellis Bay and at the base of Cornwall Bay have fully as well defined spruce belts as do the prominent south shore ridges which rise ten to twenty feet above the shore, or as the high spruce-covered sand ridge which forms the backbone of Sand Point.

These open spruce forests bear a close resemblance, both floristically and structurally, to the Great Slave Lake types. The trees are tall and spire-like, widely spaced, and branched from near the base of the trunk. The lower branches commonly rest upon the ground. The amount and nature of the ground cover depends on the degree of exposure and the nature of the substratum; and as on Great Slave Lake the latter may be divided into stony and sandy types. Since the latter are of wider occurrence they will be described first.

The most mesophytic of the sand ridge types are to be found along the south shore of the lake, where they occupy inter-ridge depressions and

small plains whose ground surfaces are protected from strong winds and are relatively near the water table. In places such areas are only a few feet wide, while in others they are spread out over a hundred feet or more. They are usually widest where streams entering the lake have built small sand plains.

PRIMARY SPP.: *Picea glauca, Betula papyrifera* var. *neoalaskana, Vaccinium Vitis-Idaea* var. *minus,* woodland mosses.

SECONDARY SPP.: *Lycopodium complanatum, Lycopodium tristachyum, Lycopodium annotinum, Lycopodium obscurum* var. *dendroideum, Cypripedium acaule, Goodyera repens* var. *ophioides, Betula papyrifera* var. *commutata,*[7] *Alnus crispa, Geocaulon lividum, Sorbus scopulina,*[8] *Rosa acicularis, Epilobium angustifolium, Aralia nudicaulis, Cornus canadensis, Chimaphila umbellata* var. *occidentalis, Ledum groenlandicum, Vaccinium uliginosum, Vaccinium canadense, Trientalis borealis, Linnaea borealis* var. *americana, Cladonia rangiferina.*

It should be noted that these narrow belts of relatively rich woods harbor a considerable number of Cordilleran and eastern species rare or otherwise unknown in our region: *Lycopodium tristachyum, Cypripedium acaule,* and the western varieties of *Betula papyrifera, Chimaphila umbellata, Sorbus scopulina,* and *Trientalis borealis.*

Ridges exposed to lake winds have a more xerophytic phase of open spruce woods. The trees are farther apart, and the ground cover changes considerably in composition.

PRIMARY SPP.: *Picea glauca, Betula papyrifera* var. *neoalaskana, Empetrum nigrum, Arctostaphylos Uva-ursi.*

SECONDARY SPP.: *Pinus Banksiana, Oryzopsis pungens, Populus tremuloides, Geocaulon lividum, Prunus pennsylvanica, Epilobium angustifolium, Vaccinium Vitis-Idaea* var. *minus, Campanula rotundifolia, Cladonia rangiferina, Cetraria islandica, Cetraria nivalis.*

This association is one of the commonest in the beach ridge vegetation, and constitutes the first above the present shore which is sufficiently stabilized to carry a forest flora. There are scores of miles of it on the south shore of Lake Athabaska, and it occasionally appears on the north shore. *Vaccinium Vitis-Idaea* var. *minus* is sometimes associated with *Empetrum* as a primary species, the whole making a thick springy mat on the sand. The crowberry fruits so heavily in August that one's shoes or moccasins soon become soaked with the juice of the berries as he walks along the ridges. *Vaccinium uliginosum* sometimes forms thick clumps on what look like old dunes.

The lakeward margins of the association merge with the shore dune types to be described later. Patches of bare sand are being partially held by the actively spreading *Empetrum* and by the roots of a group of species characteristic of such habitats: *Festuca saximontana, Festuca rubra* var. *arenaria, Poa glauca, Calamagrostis purpurascens, Tanacetum huronense* var. *floccosum,* and *Stereocaulon paschale.* On the landward side the spruces give way more or less abruptly to the jack pine woods of the back country.

[7] *Betula papyrifera* var. *occidentalis* of the Catalogue. See Rhod. 47: 312. 1945.
[8] *Sorbus sitchensis* of the Catalogue. See Jour. Arnold Arb. 20: 16–22. 1939.

The high sand ridges which lie a short distance back from the lake shore are in many places being opened by wind action. The most effective winds come from the west and northwest. Gaps thus formed usually have steep faces, and in some places they have so broken up the ridges as to give them the appearance of rows of conical hills. Topography of this sort in a "fossil" condition is to be found many miles inland south of the lake. Where the ridges have but recently been broken, typical "blowouts" are to be seen back of them. The local jack pine wood is destroyed and characteristic dune vegetation appears. An outstanding vegetational feature of such activity is the development of open park-like woods of *Picea glauca* at the *western* sides of the blowouts. It makes only a narrow fringe between the open sand and the neighboring open pine woods. This was observed repeatedly near the south shore of Lake Athabaska and was studied in some detail in the vicinity of Wolverine Point. It is one of the few situations in which the park-like spruce wood has been found away from the actual shore of the lake. The large dune area which lies just east of Wolverine Point has an extensive development of it at the western margin of the open sand (see *Plate 2*).

PRIMARY SPP.: *Picea glauca, Cetraria nivalis.*

SECONDARY SPP.: *Betula papyrifera* var. *neoalaskana, Empetrum nigrum, Arctostaphylos Uva-ursi, Cetraria islandica, Cetraria cucullata,* other lichens.

The spruces are in an exceedingly open stand and are of all ages. Most of them appear to be thriving. Blowouts are frequent in the intervening spaces and bear a flora in which *Empetrum nigrum, Polytrichum* sp., *Hudsonia tomentosa* var. *intermedia,* and certain grasses are characteristic.

That the spruce woods are not permanent is evident from the fact that they do not occur on older blowouts which have become stabilized and forested entirely with jack pine. Furthermore, they do not appear until after the blowouts are started, since they are elsewhere confined to the actual lake shore ridges. There is considerable evidence that even at the margins of the dunes they do not occupy a given area for very long. In the ecotone between spruce and pine there are many young and vigorous spruces, but no young pines. In fact the pines are obviously being destroyed, acquiring in the process a peculiarly gnarled and stunted appearance in which the branching takes on a deliquescent effect, producing rounded irregular outlines to the trees. At the open margin of the spruce strip, on the other hand, old trees are occasionally seen which are still standing but apparently on stilts, with most of the sand blown away from their root systems.

Stony shore ridges have an open stand of white spruce and birch similar in general appearance to those on sand, but the ground flora is somewhat different. The most mesophytic forest thus far studied on this type of terrain is on the complicated series of shore ridges and ancient beaches on the north side of the lake.

PRIMARY SPP.: *Picea glauca, Betula papyrifera* var. *neoalaskana, Populus tremuloides,* woodland mosses, *Vaccinium Vitis-Idaea* var. *minus, Linnaea borealis* var. *americana.*

SECONDARY SPP.: *Equisetum scirpoides, Lycopodium complanatum, Cystopteris fragilis, Juniperus communis* var. *montana, Schizachne purpurascens, Poa glauca, Oryzopsis pungens, Calypso bulbosa, Salix Bebbiana, Betula papyrifera* var. *occidentalis, Alnus crispa, Geocaulon lividum, Arenaria macrophylla, Aquilegia brevistyla, Ribes oxyacanthoides, Mitella nuda, Saxifraga tricuspidata, Amelanchier florida, Rubus idaeus* var. *canadensis, Rosa acicularis, Prunus pennsylvanica, Shepherdia canadensis, Epilobium angustifolium, Cornus canadensis, Aralia nudicaulis, Pyrola virens, Arctostaphylos Uva-ursi, Lonicera glaucescens, Viburnum edule, Campanula rotundifolia.*

The similarity between this forest and the most mesophytic phases of the open spruce woods at the eastern end of Great Slave Lake is at once apparent.   The considerable admixture of *Populus tremuloides* makes for somewhat denser woods, and is probably the result of fire.

Near the lake shore the timber is very thin and is confined to depressions between the ridges. *Picea glauca* and *Betula papyrifera* var. *neoalaskana* are still predominant, but the primary species on the ground are reduced to fruticose lichens: *Cladonia* spp., *Cetraria* spp.   Common or occasional secondary species are as follows:

Juniperus horizontalis, Festuca saximontana, Poa glauca, Salix Bebbiana, Saxifraga tricuspidata, Amelanchier florida, Rubus idaeus var. *canadensis, Rosa acicularis, Prunus pennsylvanica, Epilobium angustifolium, Pyrola asarifolia, Arctostaphylos Uva-ursi,* mosses (few), *Stereocaulon paschale.*

Isolated stands of open spruce woods have been described in other parts of the subarctic forest by J. B. Tyrrell.   His notes on some timber along the Dubawnt and Kazan Rivers (1898) indicate that it closely resembles that described above.   In another report (1896) he has this interesting observation, "One small isolated grove of White Spruce was found on a high sandy island in Hatchet Lake, standing out conspicuously in the midst of the surrounding forest of small Black Spruce."   Hatchet Lake is about 100 miles southeast of the eastern end of Lake Athabaska.   The present writer has noted park-like white spruce in the Wood Buffalo Park (1935).   There is a high sandy hill southeast of Lane Lake, about twenty miles west of the upper Slave River, which stands out prominently above the surrounding country.   The jack pine of neighboring hills and sand plains disappears on its upper slopes where there is an open timber of white spruce.   The ground cover is principally of lichens, *Cetraria nivalis, C. islandica, Cladonia alpestris,* etc., and some mat-forming heaths, *Arctostaphylos Uva-ursi* and *Vaccinium Vitis-Idaea* var. *minus.*   Blanchet (1926–C) described forests on the shores of Nonacho Lake that appear to be of open spruce backed by jack pine.   It is probable that these isolated outliers or remnants (see below) of the park-like spruce forest which now borders the Arctic tundra are occasional on sandy beaches throughout much of the jack pine country between Athabaska and Great Slave Lakes.

SUMMARY OF PARK-LIKE WHITE SPRUCE FOREST

Within the Athabaska–Great Slave Lake region an open, park-like forest of *Picea glauca,* often with the addition of *Betula papyrifera* var. *neoalaskana,* is widely distributed on ancient beach ridges and the lake shore terraces.   Around the eastern end of Great Slave Lake it spreads to the

surrounding uplands. Floristically it is rather uniform over the whole region, but locally it shows varying stages of mesophytism depending upon slope, exposure, and the character of the substratum. The most mesophytic phase usually shows a ground cover of woodland mosses, *Vaccinium Vitis-Idaea* var. *minus, Linnaea borealis* var. *americana,* and admixtures of *Vaccinium uliginosum, Ledum groenlandicum,* etc. More xerophytic phases on stony substrata have a ground flora derived largely from rock crevices, while those on sand are strongly influenced by sandy beach and dune floras.

Although most of the predominating species range throughout the whole region, the secondary species of the association change somewhat from north to south. The following species are occasional to common about Lake Athabaska, but have not been observed on the eastern arm of Great Slave Lake.

> *Lycopodium tristachyum, Lycopodium obscurum* var. *dendroideum, Schizachne purpurascens, Oryzopsis pungens, Cypripedium acaule, Goodyera repens* var. *ophioides, Betula papyrifera* var. *commutata, Mitella nuda, Amelanchier florida, Sorbus scopulina, Prunus pennsylvanica, Cornus canadensis, Aralia nudicaulis, Chimaphila umbellata* var. *occidentalis, Arctostaphylos Uva-ursi* var. *adenotricha, Vaccinium canadense, Trientalis borealis, Lonicera glaucescens, Campanula rotundifolia, Tanacetum huronense* var. *floccosum.*

Although *Pinus Banksiana* has been noted on the portage route between Great Slave and Artillery Lakes, it is so rare toward the eastern end of Great Slave Lake that it cannot be considered an important part of the flora.

On the other hand a considerably smaller number of species of northern affinity in the open spruce woods of Great Slave Lake fail to appear in those on Lake Athabaska:

> *Tofieldia palustris, Cypripedium passerinum, Dryas integrifolia, Dryas Drummondii, Hedysarum alpinum* var. *americanum, Oxytropis viscidula, Ledum palustre* var. *decumbens, Pedicularis labradorica, Solidago multiradiata, Erigeron compositus* var. *trifidus.*

Several of these northern species have been found on Lake Athabaska, but they are there strictly confined to muskegs. It is notable that over half of the northern species not found about Lake Athabaska are those which inhabit the more xerophytic phases of the spruce woods, while nearly all of the southern species that fail to extend north to Great Slave Lake represent the more mesophytic phases of the Lake Athabaska spruce. It is further notable that the richest forest on Fairchild Point — that on the tops of the hills formed of the softer sedimentary rocks — has no species which are not common on Lake Athabaska.

Two other differences between the Athabaska and Great Slave Lake types must be mentioned. One is the broad extension of open spruce woods away from the immediate shore of the lake in the more northern district. Similar situations about Lake Athabaska are invariably occupied by jack pine except at the western margins of active blowouts. The second is the failure of the open spruce forest to occupy the upper south slopes and tops of the hills of conglomerates and dolomites found on Lake Athabaska. As

stated above, the richest forest of spruce at the eastern end of Great Slave Lake grows on such sites.

Wherever the shore-forming processes of the great post-Glacial lakes have had an opportunity to work upon the pre-Cambrian sedimentary rocks, they have produced distinctive types of ancient beaches and terraces. Where the Athabaska Series or other formations of coarse-grained sandstones and quartzites have been available, as on the south side of Lake Athabaska or in parts of the eastern arm of Great Slave Lake, extensive sand deposits have been developed. The few stony beaches on Lake Athabaska made of this material are on exposed points of land where actual outcrops of the shelving sandstones occur. On Great Slave Lake the open spruce covers these sandy areas, but at Lake Athabaska the jack pine has covered nearly all of the sand except on the immediate shore of the lake. Stony beaches, on the other hand, both ancient and modern, are characteristic of areas where conglomerates, dolomites, shales, and slates outcrop. They are nearly always occupied by open spruce woods, the jack pine having been unable, for some reason, to invade them. Even on the south shore of Lake Athabaska, where the white spruce grows only on the newest of the stony beaches, the older shores are occupied by black spruce rather than by pine.

Flood Plain White Spruce Forests

The higher parts of deltas and river flood plains in the valleys of the Peace, lower Athabaska, and Slave Rivers are covered with forests of white spruce and balsam poplar (*Populus Tacamahacca*). The most mesophytic of these are pure stands of tall, clean-boled spruce. As one travels along the rivers in small boats one gets the impression of looking into a dense forest of great areal extent (*Plate 2*). This is usually not the case, for the rich woods are limited to natural levees and eddy deposits. A complicated and extensive system of wet meadows often divides the forest into comparatively narrow strips, and the levees themselves are subject to destruction by the meandering of the rivers and by the silting up of the valley floors. Buried trunks and stumps, *in situ*, are commonly seen in newly cut banks, often many feet below the present surface of the land.

Changes in land surfaces and drainage go on so rapidly in river flood plains that it is difficult to think of their forests except in terms of successional development. Stages in these successions involving marshes and wet meadows will be described under shore vegetation (see also Raup, 1935, pp. 62–85).

Forming a transition from the shore and meadow vegetation to timber is a zone of willows. On local river flood plains the willow zone is usually narrow, but in the deltas it forms broad expanses of dense shrubbery. There are two types of succession among the willows, involving different species. At slough margins the first to appear is *Salix planifolia*. This is followed by *S. petiolaris,* and then by *S. Bebbiana.* Locally formed river sand-bars, on the other hand, begin with *Salix interior* var. *pedicellata,* which is followed by *S. lutea.* A zone of *S. lasiandra* sometimes occurs

between these two.   The culmination of the development here also is with
S. Bebbiana, which persists into the forest and becomes a primary species
in the shrub layer of the flood plain timber.

The first trees to appear are the balsam, or black poplars.   Alders, *Alnus
tenuifolia*, are usually associated with the upper willows and mark a transi-
tion to the poplar forest.   The poplar association is widespread throughout
the flood plains.   It occurs in pure form or is merged with spruce in all
sorts of combinations.

PRIMARY SPP.:   *Populus Tacamahacca, Equisetum pratense, Salix Bebbiana.*

SECONDARY SPP.:   *Picea glauca* (young trees), *Salix arbusculoides, Alnus tenui-
folia,*[9] *Actaea rubra, Rosa acicularis, Rubus idaeus* var. *canadensis, Vicia americana,
Epilobium angustifolium, Aralia nudicaulis, Cornus stolonifera, Pyrola asarifolia,
Viburnum edule, Aster Lindleyanus.*

Although this list is not complete, it contains those species which are
most characteristic, and it shows the trend of the forest toward mesophy-
tism.   Young spruces germinate in the shade of the poplars, alders, and
willows, and gradually occupy larger areas.   If undisturbed the dominance
of the spruce becomes complete, so that pure stands of it are common along
the rivers.   With the coming of the spruces a loose mat of mosses is formed,
and the herbaceous flora becomes exceedingly scant.   The shrubs likewise
form a thin undergrowth, although not so scant as that in the upland spruce
wood.   The general structure of the lowland spruce wood is shown by the
following list:

PRIMARY SPP.:   *Picea glauca, Salix Bebbiana, Viburnum edule, Cornus stolonifera.*

SECONDARY SPP.:   *Equisetum pratense, Maianthemum canadense* var. *interius,
Orchis rotundifolia, Goodyera repens* var. *ophioides, Habenaria obtusata, Alnus
tenuifolia, Betula papyrifera* var. *neoalaskana, Geocaulon lividum, Actaea rubra,
Mitella nuda, Ribes oxyacanthoides, Ribes triste, Rosa acicularis, Rubus pubescens,
Rubus acaulis, Rubus idaeus* var. *canadensis, Fragaria glauca, Vicia americana,
Shepherdia canadensis, Epilobium angustifolium, Cornus canadensis, Moneses uni-
flora, Pyrola secunda, Pyrola asarifolia, Mertensia paniculata, Linnaea borealis* var.
americana, Aster Lindleyanus.

The spruce forest appears to perpetuate itself if not disturbed by fire,
clearing, or by the destruction of the land surface upon which it stands.
Young poplars do not come up in the mature spruce woods.   A frequent
mixture is one of vigorous spruces 75–100 feet tall with here and there an
ancient poplar, nearly dead and with its top gone.   When traveling or
camping in the lowland woods one not infrequently hears the loud crack
of an old poplar breaking up as it stands, and occasionally a tree is seen
falling.

UPLAND MESOPHYTIC WHITE SPRUCE FORESTS

Vast areas on the rolling upland which lies along the lower Athabaska
and lower Peace Rivers, and to the west of the valley of the Slave River,
are dominated by forests of white spruce.   These occur in their simplest
form on the Alberta Plateau as it is represented in the Wood Buffalo Park.
This is a morainic upland bounded on the east by the so-called Salt Moun-

[9] *Alnus incana* of the Catalogue.   See Rhod. 47: 333–362. 1945.

tain Escarpment and on the west by the margin of the Caribou Mountain Plateau. Its soils are prevailingly light and sandy, although some heavier soils occur near its margins. The underlying rocks are limestones of Silurian and Devonian age, the former highly gypsiferous and giving rise to a characteristic sink hole topography.

The spruce timber is found chiefly on soils of medium drainage, which usually occur on the lower slopes of hills and in hollows where there is sufficient drainage to prevent the formation of muskegs. Such conditions are most abundant in the sandy outwash and morainic country which extends from a point a few miles north of Peace Point northward and northwestward beyond the Little Buffalo River. They are probably common also in the northern area of the Wood Buffalo Park between the Little Buffalo River and Buffalo Lake, and also in the morainic country which crosses the Jackfish River south of the broad muskeg region that surrounds Conibear and Thultue Lakes.[10]   Parts of the eastern slopes of the Caribou Mountains are covered with a dense spruce forest, much of which is of small trees with an unusually scanty undergrowth.

In general the upland spruce woods have a comparatively small flora, with a much thinner undergrowth than occurs in the lowland forest (*Plate 3*). The mat of mosses and leaf-mould on the other hand is relatively thick, the former four to six inches deep and the latter as much as four inches. The secondary species are much scattered, and in places one may walk a hundred yards or more without seeing any other ground cover than the mosses. The following list will indicate the structure and composition of the forest:

PRIMARY SPP.: *Picea glauca, Salix Bebbiana, Hypnum Crista-castrensis, Hypnum Schreberi.*

SECONDARY SPP.: *Equisetum sylvaticum, Equisetum scirpoides, Lycopodium annotinum, Maianthemum canadense* var. *interius, Goodyera repens* var. *ophioides, Habenaria obtusata, Orchis rotundifolia, Corallorrhiza trifida, Calypso bulbosa, Betula papyrifera* var. *neoalaskana, Alnus crispa, Geocaulon lividum, Ribes lacustre, Ribes triste, Mitella nuda, Rosa acicularis, Shepherdia canadensis, Cornus canadensis, Arctostaphylos rubra, Pyrola asarifolia, Pyrola asarifolia* var. *incarnata, Pyrola virens, Pyrola secunda, Moneses uniflora, Linnaea borealis* var. *americana, Peltigera aphthosa.*

The spruce forests have been greatly altered by fires which have been of common occurrence from time immemorial. The main result has been the introduction of extensive stands of trembling aspen, balsam poplar, and jack pine. Aspen and pine commonly occur in pure stands, and all three appear in complex mixtures with the spruce. Studies of the effects of fire on the uplands of the Wood Buffalo Park have made it possible to designate three kinds of modification depending upon the intensity of the fire and the nature of the soils. A crown fire driven through a spruce wood by a high wind usually kills most of the trees, but it may do little damage to the moss and humus of the forest floor. In such cases the stand usually returns to spruce immediately, with the introduction of occasional pines, aspens, and

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10 Formerly known as Moose and Bog Lakes, respectively.

balsam poplars. A slower, more intense fire, on the other hand, not only kills the spruces but also spoils the chance of immediate spruce reproduction by killing off all young growth and scorching the moss mat beneath. This type of fire gives rise, on the better soils, to practically pure stands of trembling aspen, or to mixtures of aspen and pine. The aspen is a short-lived tree, which apparently does not reproduce itself when growing in dense stands. It is followed by a mixture of spruce and balsam poplar which appear in small clumps and eventually spread to cover the whole area. The poplar likewise fails to reproduce itself further and gives way to the pure spruce much as it does in the flood plain forests.

Well-developed aspen woods, with their occasional patches of spruce and balsam poplar are of wide occurrence on the uplands. Those of the Wood Buffalo Park closely resemble those of the uplands in the McMurray district except for the absence of certain species which will be noted below. The aspens form a close stand of trees fifty to eighty feet high, reaching twelve to twenty inches in diameter, with straight clean boles. A distinct shrub and young tree flora is formed mainly of willow, *Salix Bebbiana,* and sapling poplars or spruces. Other less common shrubs are *Shepherdia canadensis, Amelanchier florida, Rosa acicularis, Lonicera glaucescens, Viburnum edule,* and *Symphoricarpos albus* var. *pauciflorus.* The ground is covered with dead leaves and other plant parts, but there are almost no mosses and lichens. About thirty species of herbaceous plants occur, with none in very great numbers. The commonest is a grass, *Elymus innovatus,* which does not form a turf but is very common considering its woodland habitat.

Very intense burning on dry sites, or repeated burning at short intervals on the same site, completely destroys the plant cover. On the sandy uplands west of the Slave River this usually results in a dense pure stand of jack pine. The flora of the pine woods will be discussed in detail in another part of the paper, since it is of wide occurrence throughout the Athabaska Lake region and appears to be a primary element in the vegetation as well as a stage in the burn succession. In the latter it is apparently quite temporary and gives way directly to a pure spruce forest, sometimes without the interpolation of aspen and poplar. A commonly observed forest type is one of young vigorous spruces mixed with a scattered stand of decrepit and tottering old jack pines. With these is usually abundant evidence of burning in earlier times.

On morainic uplands in the southern part of our region, where the soils rest upon the Cretaceous strata that overlie the Paleozoic sediments, the spruce forest appears to have about the same general structure as that described above. However, just as the lowland forests here differ by the addition of the balsam fir and other eastern species, so also the upland forests are modified by the influx of a group of species which are rare or non-existent farther north. Here also the timber has been highly modified by fire, apparently in much the same manner as in the Wood Buffalo Park, with the incidence of great expanses of aspen and jack pine. The relation of the present timber to its developmental phases has not been studied, but

there is a good deal of evidence that the successions are the same as those described above.   S. H. Clark, after a forest reconnaissance of the upland northeast of Lac la Biche (1914), concluded that the small amount of spruce forest (less than one per cent in about 1650 square miles) was due to fire and the consequent development of the aspen.   Furthermore he has described briefly, in his "poplar loamy-sand-ridge" and "poplar-birch-spruce lake-slope" types what are probably developmental stages in the burn succession, and he notes that in the second of these types "the tolerant spruce promises to play an important role in the development of the climax forest." It is of interest in this connection that Richardson, in 1851, wrote that the spruce was the predominant forest tree in the upland country along his routes north of the Saskatchewan.

The following list is compiled from notes made in the vicinity of Calumet Creek, Waterways, and McMurray in the summer of 1926, the spring of 1928, and the autumn of 1935, respectively.

PRIMARY SPP.:   *Picea glauca, Populus tremuloides.*

SECONDARY SPP.:   *Dryopteris*[11] *Linnaeana, Dryopteris spinulosa, Pteretis nodulosa, Lycopodium annotinum, Lycopodium obscurum* var. *dendroideum, Pinus Banksiana, Bromus ciliatus, Oryzopsis asperifolia, Oryzopsis pungens, Schizachne purpurascens, Hierocholoë odorata, Carex Deweyana, Carex siccata, Disporum trachycarpum, Lilium philadelphicum* var. *andinum, Maianthemum canadense* var. *interius, Habenaria viridis* var. *bracteata, Salix Bebbiana, Populus Tacamahacca, Alnus crispa, Alnus tenuifolia, Betula papyrifera, Betula papyrifera* var. *neoalaskana, Corylus cornuta, Comandra pallida, Arenaria lateriflora, Stellaria longipes, Anemone cylindrica, Actaea rubra, Mitella nuda, Ribes oxyacanthoides, Rosa acicularis, Rubus idaeus* var. *canadensis, Rubus pubescens, Fragaria glauca, Prunus pennsylvanica, Prunus demissa, Amelanchier florida, Amelanchier humilis, Lathyrus ochroleucus, Vicia americana, Geranium Bicknellii, Viola rugulosa, Viola adunca, Epilobium angustifolium, Aralia nudicaulis, Cornus stolonifera, Cornus canadensis, Pyrola elliptica, Pyrola asarifolia* var. *incarnata, Pyrola virens, Arctostaphylos Uva-ursi, Vaccinium canadense, Gentiana Amarella, Agastache Foeniculum, Mertensia paniculata, Galium boreale, Galium triflorum, Linnaea borealis* var. *americana, Viburnum edule, Lonicera glaucescens, Symphoricarpos albus* var. *pauciflorus, Campanula rotundifolia, Aster conspicuus, Aster Lindleyanus, Aster laevis* var. *Geyeri, Erigeron philadelphicus, Achillea sibirica.*

It is difficult to define primary species among the shrubs, although the commonest are *Shepherdia canadensis, Prunus demissa, Viburnum edule, Corylus cornuta,* and *Rosa acicularis.*   There is probably considerable difference between the floras of north and south slopes, and, although this was not studied in detail, it can be illustrated with the distribution of the common asters.   *Aster conspicuus* is most abundant on upper northward-facing slopes, while *Aster Lindleyanus* is commonest in shady upland woods. *Aster laevis* var. *Geyeri* is common only on dry southerly slopes.

Several species in the above list reach or approach their northern limits in the lower Athabaska river region or about Lake Athabaska:

Dryopteris spinulosa, Lycopodium obscurum var. *dendroideum, Carex Deweyana, Disporum trachycarpum, Lilium philadelphicum* var. *andinum, Corylus cornuta,*

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[11] The following species of *Dryopteris* were listed in the Catalogue under the generic name *Thelypteris: Linnaeana (= T. Dryopteris), spinulosa, Robertiana, fragrans.*

Betula papyrifera, Anemone cylindrica, Prunus demissa, Pyrola elliptica, Agastache Foeniculum, Galium triflorum, Aster conspicuus.

Two of these, *Lycopodium obscurum* var. *dendroideum* and *Dryopteris spinulosa,* have been found at isolated stations in the northern part of the Mackenzie basin but appear to be rare in intervening territory. *Aster conspicuus* has been found on the eastern slopes of the Caribou Mountains, and *Anemone cylindrica* has been collected in a prairie at Peace Point, in the southern part of the Wood Buffalo Park.

It is a striking fact that only a small number of species in the forests of the lower Athabaska River region are of distinctly Cordilleran affinity. *Prunus demissa* and *Aster conspicuus* are the only ones in the above lists or in the lists of the lowland forest flora that can be so designated. To these can probably be added *Thalictrum sparsiflorum,* for which there is a record at Portage la Loche. This is in strong contrast to the conditions in the Athabaska–Great Slave Lake region proper and in the Lesser Slave Lake district to the southwest, in both of which there is a considerable Cordilleran element. The Rocky Mountain *Abies lasiocarpa* and *Pinus contorta* var. *latifolia* have both been found on the uplands about Lesser Slave Lake, and the latter has been collected on the Caribou Mountain plateau. Neither of these appears on the Cretaceous uplands of the McMurray district.

The aspen-spruce wood studied in the vicinity of Calumet Creek is distinctive for having only a single one of the species which reach the northern margins of their ranges in this district. This is *Lilium philadelphicum* var. *andinum.* It is also notable for having none of the Cordilleran species which are common about Lake Athabaska. In the latter characteristic it resembles the spruce and aspen forests of the Alberta Plateau in the Wood Buffalo Park. Two suggestions are made to throw light on these contrasts. First, the Calumet site is low in elevation above the river and occupies a depression in the dissected margin of the higher Cretaceous levels hereabouts. Second, the glacial debris upon which the forest grows rests upon a very thin layer of the Cretaceous shale or upon the Devonian limestones which outcrop along the river at this point. Such conditions may bring about notable differences in soils and drainage and may produce a habitat more nearly resembling that of the Wood Buffalo Park forest than occurs at higher levels in the McMurray district.

Spruce forests resembling those described above are almost non-existent in country east of the Paleozoic boundary. It is not impossible that representatives of them will be found as more of the area is explored, particularly to the south of Lake Athabaska or on small local flood plains farther north. The only woods seen thus far which at all resemble these spruce types are near the northwest shore of Lake Athabaska. Along a small stream which enters the lake a short distance northeast of Sand Point there is a small piece of timber which has the general appearance of the simpler upland types west of the Slave River. The stream drains through pine-covered sand plains and comes from muskeg and lake areas farther

inland.   The spruce is confined to what appear to be small local plains in the narrow valley of the stream.   The soil is very sandy and gravelly.

PRIMARY SPP.: *Picea glauca, Betula papyrifera* var. *neoalaskana.*

PROMINENT SECONDARY SPP.: *Alnus crispa, Goodyera repens* var. *ophioides.*

The moss mat is three to four inches thick, over a layer of raw humus about two inches thick.   The spruces are one to two feet in diameter, and the birches up to a foot.   No list of secondary species was made, but the shrub and herb floras were noted as extremely scant, not unlike those described on page 46.   The presence of *Alnus crispa* in considerable amounts and the thick moss and humus layers relate it also to this type.

JACK PINE FORESTS

Forests of Banksian or jack pine (*Pinus Banksiana*) are abundant in the southern and central parts of our region.   The northeastern limits of the pine as a species are not far short of the limits of the forest itself.   It has been noted at Selwyn and Theitaga Lakes in the Dubawnt drainage (Tyrrell, 1897), and at Kipling Lake northeast of Great Slave Lake (J. W. Tyrrell, 1901).   Preble noted it as common on the Simpson Islands in Great Slave Lake, and also about the northern arm of this lake (1908). He also saw it on his route between Great Slave and Great Bear Lakes, but states that it is rare north of the height of land.   It has been noted on the Mackenzie as far northward as 64° 30′ (Richardson, 1851).

The northern limits of the jack pine as a primary element in the forest are not so well known, but they appear to fall far short of the limit of trees (see map, *Fig. 5*).   The pine is characteristic over large land areas around Lake Athabaska and west of the Slave River.   It is common about the western arm of Great Slave Lake (Cameron, 1921), and Harper's descriptions (1931) of the Tazin and Taltson region show that it is a predominant species on sand plains and rocky hills throughout that area.   Around much of the eastern arm of Great Slave Lake, however, its place is taken by white spruce.   Judging by Blanchet's notes the boundary south of the east arm must be somewhere between Nonacho Lake and Lake Eileen (1926–C).

The pine woods may be described in two phases which are closely correlated with the substrata upon which they are found — sandy plains or ridges, and rocky hills of granite or very hard metamorphic rock (*Plates 3, 4*).   In both types the primary tree is clearly the jack pine, though in some places the white birch commonly occurs.   Primary species in the ground layers of both types include *Arctostaphylos Uva-ursi, Cetraria nivalis,* and *Cladonia rangiferina.*   Beyond this the similarity does not go, and one meets with striking differences among both primary and secondary species.   On rocky hills *Picea glauca* is sometimes abundant, and in the lower strata *Artemisia frigida, Amelanchier florida,* and *Saxifraga tricuspidata.*   The last is exceedingly common as a primary species on the ground. None of these four occur as primary species on sandy soil.   On the latter *Alnus crispa, Picea mariana, Vaccinium canadense,* and *V. Vitis-Idaea* var. *minus* commonly grow in this capacity.   The contrasts between the primary floras of the two types may be summarized as follows:

PRIMARY SPP.: Common to both rocky and sandy woods: *Pinus Banksiana, Betula papyrifera* var. *neoalaskana, Arctostaphylos Uva-ursi, Cladonia rangifer.na, Cetraria nivalis.* Rocky woods: *Picea glauca, Amelanchier florida, Saxifraga tricuspidata, Artemisia frigida.* Sandy woods: *Picea mariana, Alnus crispa, Vaccinium canadense, Vaccinium Vitis-Idaea* var. *minus.*

The SECONDARY SPECIES of the jack pine woods may be treated in the same manner. A list of those commonly found in either type is as follows: *Lycopodium annotinum, Festuca saximontana, Poa glauca, Agrostis scabra, Calamagrostis purpurascens, Elymus innovatus, Carex siccata, Maianthemum canadense* var. *interius, Goodyera repens* var. *ophioides, Populus tremuloides, Salix Bebbiana, Geocaulon lividum, Pulsatilla ludoviciana, Rosa acicularis, Fragaria glauca, Prunus pennsylvanica, Shepherdia canadensis, Epilobium angustifolium, Aralia nudicaulis, Galium boreale, Lonicera glaucescens, Linnaea borealis* var. *americana, Campanula rotundifolia, Solidago decumbens* var. *oreophila, Hieracium canadense, Polytrichum juniperinum, Cladonia alpestris.*

Species found thus far only in sandy pine woods: (1) Wide-ranging species of rich woods: *Lycopodium complanatum, Lycopodium obscurum* var. *dendroideum, Empetrum nigrum, Cornus canadensis, Ledum groenlandicum, Vaccinium uliginosum, Viburnum edule, Peltigera aphthosa, Hypnum Crista-castrensis, Hypnum Schreberi.* (2) Species of dry or rich woods, but here found at the margins of their ranges: *Oryzopsis pungens, Panicum subvillosum, Cytripedium acaule, Salix Scouleriana, Lechea intermedia* var. *depauperata,*[12] *Hudsonia tomentosa* var. *intermedia.*

Species found thus far only in rocky pine woods: *Woodsia ilvensis, Cryptogramma crispa* var. *acrostichoides, Polypodium virgin.anum, Dryopteris fragrans, Dryopteris Robertiana, Lycopodium clavatum* var. *megastachyon, Juniperus communis* var. *montana, Juniperus horizontalis, Poa palustr.s, Calamagrostis canadensis, Schizachne purpurascens, Allium Schoenoprasum* var. *sibiricum, Anemone multifida* var. *hudsoniana, Stellaria longipes, Arenaria verna* var. *pubescens, Arenaria dawsonensis, Corydalis sempervirens, Draba aurea, Arabis lyrata, Arabis Holboellii* var. *retrofracta, Heuchera Richardsonii, Ribes oxyacanthoides, Ribes glandulosum, Rubus idaeus* var. *canadensis, Potentilla tridentata, Potentilla arguta, Potentilla multifida, Potentilla pennsylvanica, Potentilla nivea, Geum triflorum, Lathyrus ochroleucus, Androsace septentrionalis, Symphoricarpos albus* var. *pauciflorus, Antennaria campestris, Antennaria nitida, Antennaria rosea, Achillea Millefolium, Arnica lonchophylla, Senecio cymbalarioides* var. *borealis.*

The jack pine forest is the simplest, floristically, of any of the woodlands of our region. The rather long lists given above are composite ones formed from studies in several different regions in the Wood Buffalo Park and around Lake Athabaska. When a single site is considered by itself it is commonly found to have a very small number of species. This condition reaches lowest terms on some sand plains observed near Wolverine Point on the south shore of Lake Athabaska, where the primary species are *Pinus Banksiana, Vaccinium canadense,* and *Cladonia rangiferina (Plate 4).* After a careful examination of a large area only half a dozen vascular species could be found among the secondary flora; and over whole acres the pine is the *only vascular plant,* with not even the blueberry appearing. The forest is open and park-like, with trees seventy years old. *Empetrum nigrum* occasionally appears as a mat about the bases of the trees. The ground is clothed with fruticose lichens.

[12] See Rhod. 40: 127, 129–130. 1938.

At the other extreme the sandy pine woods approach a mesophytic condition. *Betula papyrifera* var. *neoalaskana, Alnus crispa,* and *Picea mariana* become prominent; and on the ground the lichens and blueberries are in large part replaced by mats of woodland mosses and *Vaccinium Vitis-Idaea* var. *minus.* *Ledum groenlandicum, Arctostaphylos Uva-ursi, Alnus crispa, Cornus canadensis, Empetrum nigrum, Goodyera repens* var. *ophioides, Melampyrum lineare, Lycopodium annotinum, Viburnum edule* and *Cladonia alpestris* become common.   In the Wood Buffalo Park forest of this type appears to develop into one of white spruce, but in the pre-Cambrian country no evidence for such a development was observed (*Plate 4*) (see below for further discussion of developmental trends).

The sandy pine wood occasionally shows a very wet phase at the margins of ponds or lakes.   Here the pine is growing in a dense stand of bog shrubs such as *Vaccinium uliginosum, Ledum groenlandicum, Chamaedaphne calyculata, Andromeda Polifolia,* and *Kalmia polifolia.*   Characteristic bog or marsh herbs appear also: *Calamagrostis canadensis, Spiranthes Romanzoffiana, Lycopus uniflorus.*

A very dry phase is to be found at the western margins of dunes and blowouts on the south side of Lake Athabaska, or on occasional beach ridges on the northwest shore.   Here the pines are reduced to a decrepit condition, much gnarled and twisted.   The sand about them is partly in motion, and partly fixed by fruticose lichens or occasional shrubs.   This is the condition in which the pine woods are invaded by park-like white spruce, as previously noted.

The pine woods of the rocky hills, except for their lichen and moss components, are composed largely of a crevice flora (*Plate 3*).   Areas of soil are usually small and of gravelly morainic materials.   The rocks have not weathered sufficiently to produce a residual soil, so that the principal plants on the vast surfaces of exposed rock are lichens and mosses.   Where the slopes are at all steep these are limited to such species as can attach themselves to the rock, while on gentle slopes and hilltops unattached fruticose lichens appear in great abundance (See L. C. Raup, 1930).   The association is fairly uniform over most of the granitic parts of the pre-Cambrian country which fall within the range of prominence of the jack pine.   It has outliers in the lowlands of the eastern part of the Wood Buffalo Park (Raup, 1935), and it covers those parts of the ancient metamorphosed sedimentary rocks in the Laurentian country which are too hard to have produced a residual soil since they were exposed.

As would be expected from the nature of the substratum this phase of the pine forest is exceedingly open and "scrubby."   Most of the vascular flora is in small patches of gravelly till or in rock crevices of varying dimension and aspect.   A common sight is a long row of shrubs or ferns, straight as though planted, extending for many yards over a hillside.   On either side of the row, which occupies a crevice, will be only the bare or lichen-covered rock.   The granitic rocks tend to break up into rhombohedrons, so that surface markings on the glacially scoured hills most commonly assume the form of triangles of all shapes and sizes, with here and there a rhom-

boidal figure. The vascular flora, therefore, is laid out in strangely regular geometrical patterns. The abundance of fruticose lichens gives the whole rockscape a grayish color in dry weather; but with a little moisture the yellow, orange, cream, and curious sea-green hues of the lichens transform the picture to one of surprisingly bright tints.

An analysis of the associational and geographical affinities of the floras of the two types of pine woods leads to further contrasts. It will be noted that in the above lists the secondary species limited to the sandy woods are divided into two groups: 1, wide-ranging species of rich woods; 2, species of dry or rich woods, here found at the margins of their ranges. Of the species limited to rocky pine forests, practically none are characteristic of rich woodlands, and very few are either notable range extensions into the region or conspicuously at the margins of their ranges. This suggests that mesophytism develops faster in the sandy than in the rocky woods, and that, possibly due to greater local variability, the sandy habitat is more attractive to selective species than the rocky one.

Much of the rocky woodland flora proves at once to be characteristic of dry upland woods and crevices throughout wide areas in boreal America. One notable local parallelism must be stated, however. Over half of its species (51%) also occur in the natural prairies of the Wood Buffalo Park and the Peace River country. A list of these species would include such prominent grasses as *Calamagrostis canadensis* and *Schizachne purpurascens,* and such abundant prairie shrubs and herbs as *Ribes oxyacanthoides, Symphoricarpos albus* var. *pauciflorus, Heuchera Richardsonii, Potentilla arguta, Geum triflorum, Lathyrus ochroleucus,* and *Antennaria campestris.* If only those species are considered which are limited to the rocky pine woods, the percentage common to the prairie is a little greater (56%). By contrast something less than 26% of all the species of the sand plain pine woods also grow in the prairie, and *none* of those which are limited to the sandy woods.

The significance of the prairie affinity of the rocky woodland flora is not evident, but it is clear that it heightens the contrast between the two types of jack pine forest.

Still another kind of analysis of the pine woods is suggestive. Notes on the rocky woodland were derived principally from three regions: the granitic hills of the Peace River delta and the upper Slave River, the hills in the neighborhood of Shelter Point, Lake Athabaska, and those near Charlot Point. Of all the species listed, sixteen were noted in all three regions, twenty-three in two of the regions, and thirty-seven in only one district. Of those common to all three areas 31% were limited to rocky woods; of those common to two areas 48% were so limited; and of those growing in only one of the three districts over 70% were characteristic of rocky woods. Figures from the sandy woods produce somewhat similar results. Of ten species growing in four of the seven areas studied, 20% were limited to sandy woods; and of seventeen species growing in only one of the seven areas, 30% were characteristic.

Two suggestions may be derived from these data: 1, many more species

are only occasional in the jack pine woods than are common in them; 2, the plants which are found only occasionally in one or the other of the two types are much more likely to be limited to it and characteristic of it than those which are common there.

Recurring fires have undoubtedly facilitated the spread and establishment of pine forests in our region. In some places, such as on the better soils of the Wood Buffalo Park, fire has sometimes so completely destroyed spruce or aspen woods as to give rise to new stands of jack pine. In fact all stages in the burn succession can be seen, as noted earlier in the paper. These developmental stages are not evident in the pre-Cambrian country, however, and it seems clear that large areas have a natural forest of jack pine which for the time being at least is succeeding itself. I have seen ancient pine woods in the dune region south of William Point, Lake Athabaska (*Plate 4*) which have reached great age, and in which there is little or no evidence of fire.

Where the pine wood is burned off it immediately comes back to pine. The aerial photographs of the sandy country around Wolverine Point, Lake Athabaska, show an anomalous meadow-like appearance over considerable districts. Upon examination these surfaces proved to be clothed with a nearly pure stand of young jack pines one to eight feet high. Many which have reached a height of only one to three feet and a diameter of half an inch are twelve to fifteen years old and fruiting heavily. A study of these pines over a couple of square miles showed three, or perhaps four stages of development following a series of burns.

Large areas are characterized by stands of the small trees twelve to fifteen years old, one to three feet high. Among these are rather thick stands here and there (and sometimes standing singly) of trees six to eight feet high, about two inches in diameter at the base, and about forty years old. A still older stand of pines occurring occasionally showed trees about eight inches in diameter at the base, thirty feet high, and 120 years old. Trees intermediate in size between the last two are sometimes met with. It may be deduced that the country was partly burned off about fifteen years ago, the pines burned then being about twenty-five years old. The remains of this twenty-five-year-old stand are lying everywhere on the ground, many of them still undecomposed so that their rings may be counted. A considerable portion of this stand escaped the fire, however, and is now about forty years old. There must have been a major conflagration, then, about forty years ago, which destroyed a much older stand. Among the remains on the ground are stems two to three inches in diameter which may represent the generation of the 120-year-old trees or of the intermediate age mentioned above, and which escaped the fire of forty years ago but not that of fifteen years ago. In any event, there is no evidence of change in composition throughout a long period, and in the face of repeated destructive fires.

Balsam Fir–White Spruce Forests

The most mesophytic forests of the Athabaska–Great Slave Lake region are in the extreme southern part and are dominated by a mixture of white

spruce (*Picea glauca*) and balsam fir (*Abies balsamea*).   These constitute a phase of the wide-ranging fir-spruce belt which extends to northern New England and the Gulf of St. Lawrence.   In the Cordilleran region the balsam fir is replaced by the alpine fir, *Abies lasiocarpa*.   *Abies balsamea* reaches its western limits somewhere in the central Athabaska River country, while *A. lasiocarpa* is known east of the mountains only at isolated stations such as in the Lesser Slave Lake district (See Halliday and Brown, 1943).   Within our region the fir is common enough to be regarded as a primary species only along the Clearwater and lower Athabaska Rivers (*Plate 2;* also map, *Fig. 5*).   On the latter Robert Bell (1884, p. 8) mentions the fir as a part of the timber between Lac la Biche and Pelican Rivers, and William Ogilvie (1885, p. 51) says that it is only occasional between Lesser Slave Lake River and McMurray.   From these notes we may gather that the balsam fir becomes reduced to secondary significance as one ascends the Athabaska from McMurray in the same way that it disappears at the Athabaska delta.

My own observations indicate that the spruce-fir forest is confined to the immediate valleys of the streams, and to local terraces within the valleys. John Richardson (1851, Vol. 2, p. 272) designates spruce as the chief upland tree north of the Saskatchewan and mentions the balsam fir only among those species which are abundant "on the alluvial borders of rivers and lakes."   It is abundant on such sites about Waterways and McMurray and down the Athabaska at least as far as the mouth of the Firebag River; but in the heavy forests at the head of the delta it is only occasional.   I have not seen it any farther north than this, though it has been reported probably erroneously as far as lat. 62° by Richardson (1823, p. 214).   It was also noted in the gorge of the Little Buffalo River by Camsell (1903, p. 159A), but this record also is not verified.   I have not seen it at the mouths of any of the lesser streams which drain into the south side of Lake Athabaska, although it may yet be found there.   J. B. Tyrrell states (Sci. 22: 76–77. 1893) that the balsam fir "grows to a large size among the white spruce on the top and sides of Duck Mountain in Manitoba, and between the Saskatchewan and Churchill rivers in the District of Saskatchewan.   It extends for a short distance north of the Churchill River, where it appears to reach its northern limit."   It is also of interest that the fir was not noted by Tyrrell or Dowling in their extensive travels between Cree and Athabaska Lakes (Tyrrell, 1896), although copious notes on forest types are to be found in their descriptions.

The northeastern boundary of the spruce-fir forests in the region south of Lake Athabaska bears some relation to the division between the "Mixedwood" section and certain phases of the "Northern Coniferous" section of the Canadian forest as outlined by Halliday (1937, pp. 19–21).   It would probably be necessary to move Halliday's line somewhat to the northeastward, to include more of the Clearwater and lower Athabaska valleys in his Northern Coniferous section.   The correlation does not exist farther northward, however, since this author makes no distinctions within the "Mixed-

wood" type in all the region between southern Manitoba and the Liard.

The following list will show the general structure of the spruce-fir forest as it appears along the lower Athabaska.

PRIMARY SPP.: *Picea glauca, Abies balsamea, Betula papyrifera* var. *neoalaskana.*

SECONDARY SPP.: *Dryopteris Linnaeana, Pteretis nodulosa, Equisetum pratense, Maianthemum canadense* var. *interius, Cinna latifolia, Orchis rotundifolia, Habenaria obtusata, Habenaria hyperborea, Calypso bulbosa, Listera borealis, Corallorrhiza trifida, Alnus tenuifolia, Caltha palustris, Thalictrum venulosum, Mitella nuda, Ribes triste, Ribes hudsonianum, Rubus pubescens, Rosa acicularis, Rhamnus alnifolia, Viola palustris, Viola renifolia* var. *Brainerdii, Epilobium angustifolium, Aralia nudicaulis, Cornus stolonifera, Pyrola asarifolia* var. *incarnata, Pyrola virens, Pyrola secunda, Trientalis borealis, Viburnum edule, Linnaea borealis* var. *americana.*

The woods are quite wet in the early part of the season, with frequent pools of standing water. Most of the surface is subject to flood in the spring. When we visited the lower Firebag River early in June, 1935, the water must have but recently subsided after having backed up from the main channel of the Athabaska. The ground surface was caked with mud, as were also the tree trunks and branches to a height of six or eight feet. The banks of the river and all of the lowland woods were strewn with drift timber and miscellaneous debris.

The trees often reach considerable size, one to two feet in diameter and 100 feet tall. There is a rather thick mat of woodland mosses, and the shrub layer, consisting principally of *Alnus, Cornus,* and *Viburnum,* is relatively dense compared with that of the upland woods. Characteristic plants of pools and their margins are *Caltha palustris, Rhamnus alnifolia, Ribes triste, Viola palustris, V. renifolia* var. *Brainerdii,* and *Alnus tenuifolia.*

Although most of the species listed above are widely distributed in the spruce forests of Canada, yet several here approach or reach their northern limits in the Mackenzie basin. *Rhamnus alnifolia* has been found nowhere else in the entire basin, and neither *Cinna latifolia* nor *Pteretis nodulosa* have been collected north of the Athabaska delta. *Coptis groenlandica* and *Trientalis borealis* are occasional in rich woods about Lake Athabaska but are not known farther north.

BLACK SPRUCE–LODGEPOLE PINE FORESTS

Although a northern Cordilleran floristic influence is distinctly noticeable in the Athabaska Lake country, the only part of our region which is known to have an outlier of northern Rocky Mountain or foothill forest types is the Caribou Mountain Plateau north of the lower Peace River (see map, *Fig. 5*). Here a timber of *Picea mariana* and *Pinus contorta* var. *latifolia* with a thick mat of woodland mosses is common (Raup, 1935, pp. 21–22). It is possible that this forest is also growing on other erosion plateaus of Cretaceous rock such as the Birch Mountains, the Buffalo Head Hills, and possibly the Eagle Mountains, but none of these uplands has been examined botanically. Lodgepole pine woods are found on the uplands about Lesser Slave Lake, and in the Notikewin district north of the Peace River (Raup, 1934; Halliday, 1937). Mixed forests of black spruce, lodgepole pine, and

white spruce are widespread along the Alaska Highway between Fort St. John and Summit Pass (Raup, 1945).

Lodgepole pines were observed in our region near the top of the eastern slope of the Caribou Mountains, but they were not studied extensively. The elevation here is about 2000 feet above sea-level. The pine is most abundant on semi-open knolls which it shares with black spruce. Large areas on the upper slopes of the Caribou Plateau are covered with a dense forest of black spruce mixed with a few birches, *Betula papyrifera* var. *neoalaskana,* and a rather abundant growth of *Alnus crispa.* The moss mat is very deep and there is a scattering of the usual shady woodland herbs: *Equisetum sylvaticum* var. *pauciramosum, Calypso borealis, Pyrola secunda, Mitella nuda,* and *Lycopodium annotinum.* In the more open conditions mentioned above the ground cover is dominated by a lichen mat of *Cladonia rangiferina* and *Cetraria nivalis.* In several places decrepit old pines appear, entirely surrounded by dense thickets of black spruce, suggesting that the latter have arisen in the course of a succession.

There is reason to believe that the black spruce–lodgepole pine woods are not only on the highest, but also the oldest land surfaces in our region. The hills would have risen above the 1600-foot post-Glacial lake level, and are comparable in age to the Cretaceous plateau surfaces west of the lower Athabaska River. As I have noted previously (1935) there are some clayey, boulderless soils on the Caribou Plateau which may be residual. They contrast strongly with morainic deposits on the eastern slopes. This condition suggests that the plateau summit was not all cleaned off by the latest of the Pleistocene ice advances. Part of it may, however, have been submerged for a portion of post-Glacial time under great lakes whose levels rose far above 1600 feet. Soil studies in the Peace River agricultural region (Allan, 1919; Rutherford, 1930) indicate that most of the materials on the long gentle slopes between the uplands and the deep river valleys were laid down in fresh-water lakes; and since these surfaces lie mostly above 2000 feet, it is possible that only the highest parts of the Caribou Plateau remained above water. At any rate, it is not impossible that the highest surfaces on the Caribou Mountains and other Cretaceous plateaus served as refuges or early invasion areas for northern Cordilleran forests during the latest phase of the Pleistocene and during the period of great glacial lakes which followed. They could then have served as centers for the dispersal of Cordilleran species in our region.

Bog Forests

Bog forest constitutes one of the commonest types of timber in the Mackenzie basin. It probably covers more land surface in the pre-Cambrian portions of the Athabaska–Great Slave Lake region than it does farther westward. This follows from the facts that the development of a bog type of vegetation, or muskeg, in our region is dependent upon the presence of some sort of undrained depression in which a supply of moisture is available, and that this type of topography is especially common in the Laurentian country. The succession of vegetation set up in these depres-

sions usually involves characteristic mosses and bog shrubs, and culminates in a forest of black spruce, sometimes accompanied by larch. Almost invariably there is a shrub layer primarily of Labrador tea (*Ledum groenlandicum*) and a thick mat of mosses which are usually arranged in hummocks (*Plate 5*). In the wetter condition the mosses are *Sphagnum*, but in drier ones they are woodland species of *Hypnum*. Everywhere the forest is of small stature, the larger trees reaching heights of thirty to fifty feet.

The structure and flora of the bog forest may be characterized as follows:

PRIMARY SPP.: *Picea mariana, Ledum groenlandicum, Sphagnum sp., Larix laricina.*

SECONDARY SPP.: *Equisetum sylvaticum* var. *pauciramosum, Equisetum scirpoides, Carex gynocrates, Carex disperma, Carex media,*[13] *Carex capillaris, Eriophorum opacum, Maianthemum canadense* var. *interius, Habenaria hyperborea, Habenaria obtusata, Orchis rotundifolia, Listera borealis, Corallorrhiza trifida, Spiranthes Romanzoffiana, Salix pyrifolia, Salix glauca, Salix myrtillifolia, Betula papyrifera* var. *neoalaskana, Betula glandulosa, Geocaulon lividum, Ranunculus lapponicus, Ranunculus Gmelini* var. *Purshii,*[14] *Drosera rotundifolia, Parnassia palustris* var. *neogaea,*[15] *Ribes hudsonianum, Ribes triste, Mitella nuda, Rubus acaulis, Rubus Chamaemorus, Cornus canadensis, Moneses uniflora, Pyrola secunda, Pyrola asarifolia, Pyrola virens, Chamaedaphne calyculata, Arctostaphylos rubra, Vaccinium Oxycoccus, Vaccinium Vitis-Idaea* var. *minus, Vaccinium uliginosum, Linnaea borealis* var. *americana.*

The selection of a group of secondary species to represent the muskeg habitat is difficult for several reasons. As noted above the bog forest is the result of a hydrarch successional series. Stages which immediately precede the forest are wet and swampy, with open areas of mosses and sedges or bog shrubs. Remnants of these stages persist into the bog forest and make it difficult to draw satisfactory lines between swamp and forest. Such aquatic groups as the sedges are probably inadequately selected in the above list on this account.

Furthermore, the list of secondary species is not entirely complete for our region. It is composed of those forms noted as common in muskegs of at least two areas studied, and therefore it does not include a few species which are geographically somewhat limited. There is a small group, for instance, which appears around the eastern arm of Great Slave Lake or on the bleaker parts of the north shore of Lake Athabaska: *Tofieldia palustris, Rhododendron lapponicum, Vaccinium uliginosum, Pinguicula villosa, Boschniakia rossica.* Another group is allied to these geographically, but its members appear rarely or occasionally on the uplands of the country west of the Slave River: *Carex concinna, Ranunculus lapponicus, Ledum palustre* var. *decumbens, Andromeda Polifolia, Pedicularis labradorica. Alnus crispa,* which is typical of rich upland woods throughout most of the region, becomes a common shrub of muskeg forest at the eastern end of Great Slave Lake.

[13] *Carex Vahlii* var. *inferalpina* of the Catalogue.

[14] *Ranunculus Purshii* of the Catalogue. See Rhod. **41**: 385–386. 1939.

[15] *Parnassia multiseta* of the Catalogue. See Rhod. **39**: 311. 1937.

Further difficulties in determining the floristic confines of our muskeg forest appear when its southern and southwestern relationships are considered. I have already noted (1935) that in the Wood Buffalo Park transition stages are sometimes evident between bog forest and the upland white spruce forest of the region. Questions here arise as to whether such typical woodland species as *Shepherdia canadensis, Viburnum edule,* and *Salix Bebbiana,* which are likely to occur in mossy forests of black spruce, are to be considered parts of the bog forest community. A considerable study of the bog forest type, however, shows that they do not appear except in these transition stages, and had best be related to the forest type which they seem to presage.

There are very few muskeg species in the lower Athabaska River region which fail to extend far northward at least in the Paleozoic or Cretaceous regions. *Rhamnus alnifolia,* which occupies muskeg habitats in the lowland woods along the Athabaska, apparently goes no farther northward, and some of the species of rich woods already mentioned may also be found in muskegs: *Cinna latifolia, Trientalis borealis.* When the whole flora is taken into consideration a considerable number of species do not extend east of the boundary between the Paleozoic and pre-Cambrian rocks. When the bog forest is considered alone, however, this is not the case, and a very small number appear to be so restricted. Representative of these are *Listera borealis, Caltha palustris,* and possibly *Ribes lacustre.* The last has been found in the pre-Cambrian region only on dolomitic rocks north of Lake Athabaska. There is some evidence of a change in flora as one goes northeastward toward the limit of trees. Field notes made about the eastern arm of Great Slave Lake show that *Larix* is more abundant than southward, and that it may sometimes be classed among the primary species. The prominence of *Alnus crispa* in the shrub layer here has already been mentioned.

These notes suggest the same conclusions concerning the bog forests that were reached in studies of the Peace River and Wood Buffalo Park regions (Raup, 1934; 1935): that the type is essentially uniform throughout the entire region, both structurally and floristically. The few secondary species which are geographically limited follow the same demarkation lines marked by the other elements in the flora.

The muskeg habitat which finally gives rise to the bog forest is a physiographic-climatic phenomenon, and the development of the muskegs is dependent upon the existence of undrained depressions and the presence of peculiarly adapted peat-forming mosses which rapidly colonize the open water of lakes and ponds. First among glacial and physiographic causes for undrained depressions are glacial plucking and scouring. These are especially obvious in the pre-Cambrian districts where morainic materials are sparse and do not mask the country rock. Such rock depressions vary in size from small pools a foot in diameter to large lakes. Most of the larger lakes appear to occupy the basins of pre-Cambrian drainage systems, but the latter have been so modified that the ancient lines are now scarcely

visible.   Many depressions have been formed by morainic dams across
main drainage lines.   One of the most conspicuous of these is the basin of
Conibear (Moose) Lake in the Wood Buffalo Park (Raup, 1935).   The
continued fall of water levels in the great lakes has produced such charac-
teristic shore phenomena as barrier beaches which impound lagoons.   In
the vicinity of Shelter Point, on the north shore of Lake Athabaska, there
is a long series of these beaches in a "fossil" condition, reaching several
miles inland.   The intervening lagoons are in various stages of muskeg
development.   Similar conditions are common along the south shore of
Lake Athabaska.

Sand and mud bars along the lower reaches of the great rivers, such as
the Athabaska, Peace, and Slave, often subtend, either on islands or on the
shore, extensive lagoons and meadows.   These usually produce a reed
swamp vegetation which develops a typical flood plain forest.   Occa-
sionally, however, drainage is cut off in such a way that a muskeg develops
instead, and this results in bog forest with a mixture of plants from rich
flood plain woods.   Such a muskeg has been studied along the Athabaska
River near Calumet Creek, on the mainland back of Wheeler's Island.

Another influence which greatly affects the presence or absence of
muskegs is the configuration of underlying sedimentary rock strata.
Where these are nearly level or only slightly tilted, as on the Athabaska
Sandstones, a bog forest type of vegetation occupies nearly every crevice
(*Plate 5*).   This can possibly be accounted for by the rather free move-
ment of water along joint planes and the consequent formation of "pools"
above the levels of permanent frost in the crevices.   The same phenomena
may be seen where the softer portions of the Tazin series outcrop on the
north shore of Lake Athabaska, and where the ancient sediments appear
about the eastern arm of Great Slave Lake.   The configuration of the strata
near the tip of Fairchild Point shows this clearly.   The steep ledgy slope
on the north side of the hill is covered with small bog forest, developed on
the ledges whose floors dip to the south, while the south slopes are dry and
breaking up into masses of slide rock and talus.   The same arrangement can
be seen on Charlot Point, Lake Athabaska.   A special case related to this
category is to be seen in the Wood Buffalo Park where the flat-lying Silurian
limestones are cavernous and give rise to sink holes.   Where these holes
have subsequently been plugged, or otherwise given a permanent water
level, they have developed typical muskegs.

The significance of permanent soil frost in the formation of muskeg habi-
tats has already been discussed.   Even in mid-summer the frost-line in
muskegs is never far below the surface, perhaps two to three feet at most;
and in the autumn (late August and early September) the mossy bogs are
the first to freeze.

DISTRIBUTION AND GEOGRAPHIC AFFINITIES OF THE FORESTS

The accompanying map of forest types (*Fig. 5*) is far from complete,
and its boundaries must be looked upon as tentative; nevertheless I believe
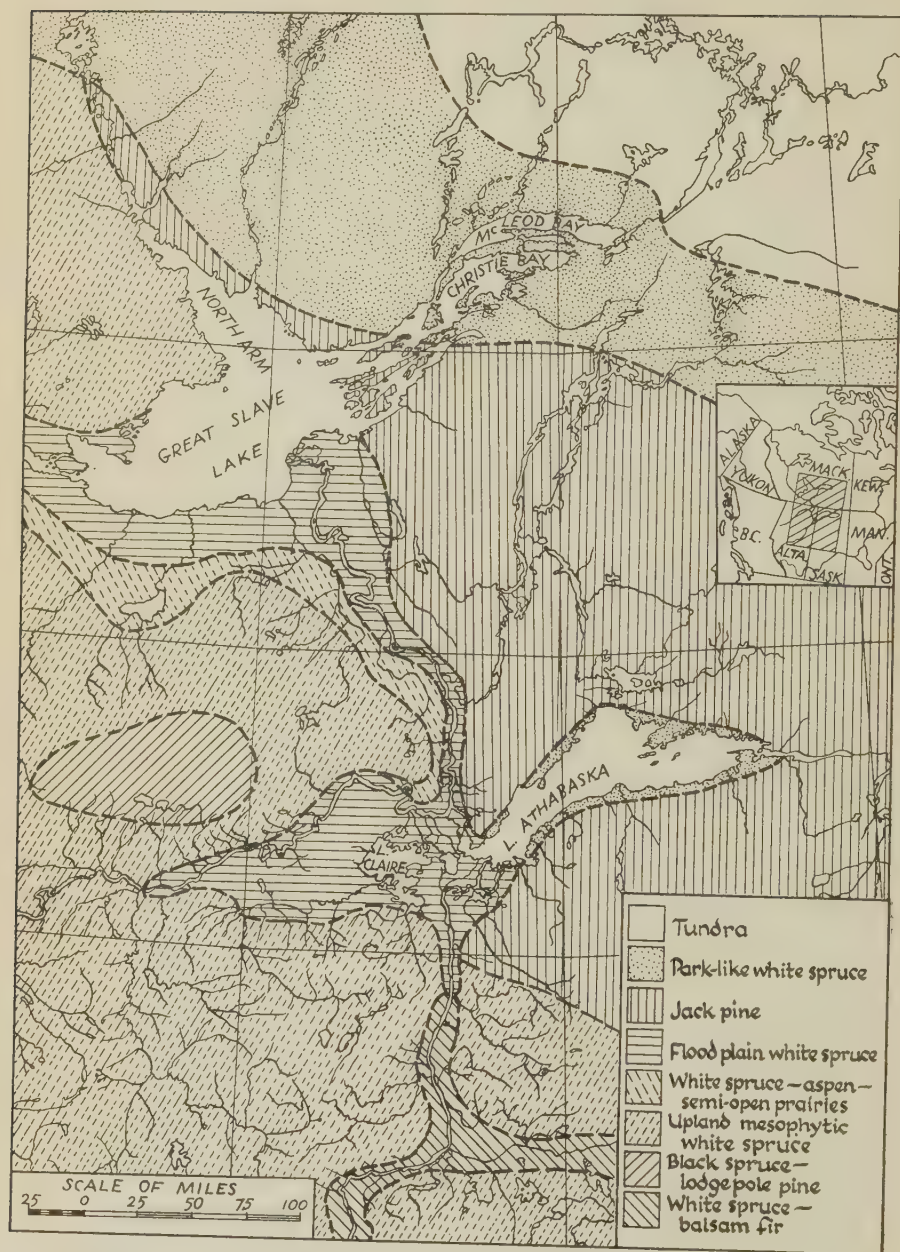the disposition of its principal areas is sufficiently near the truth to serve

Fig. 5. Map of the principal forest types in the Athabaska–Great Slave Lake region.

for the correlations that follow. These correlations appear when the map is superposed upon others which show the arrangement of geological formations and the effects of glaciation. Due to the youth of the land surface this can be regarded as a correlation with soil factors; and due to the existence of a recognizable sequence of post-Glacial events, a time element can be inserted. A third set of factors, those of climate, is more difficult of comparison, and must be used only in the most general terms. Finally, it will be useful to examine the present distribution of our forest types in the light of the Pleistocene and post-Pleistocene history of the species of which they are made.

CORRELATION WITH GEOLOGICAL FORMATIONS AND AGE OF SURFACE (Compare maps, *Figs. 2, 4*)

Park-like white spruce timber is characteristic of the most youthful surfaces in the pre-Cambrian area: those exposed at the final disappearance of the ice and the formation of the 700-foot post-Glacial lake. Most of these surfaces are approximately equivalent in age to the Mackenzie Lowland, and they occupy a broad strip of country covering most of the Yellowknife, Lockhart, and upper Thelon drainage basins, as well as the country around Christie and McLeod Bays in Great Slave Lake. The type also appears here and there on sandy and stony beaches around Lake Athabaska and northward. It has also been found sporadically on high sand hills west of the Slave River where it is on somewhat older surfaces.

Flood plain spruce forests may occur anywhere in the region on recent silt deposits along streams, but they are concentrated in the Mackenzie Lowland physiographic province, all of which is below the shores of the 700-foot post-Glacial lake. Thus they are, with the possible exception of the more recent raised beaches on Great Slave and Athabaska lakes, on some of the youngest surfaces which the region affords.

Upland mesophytic forests of white spruce predominate on most of the surface which is underlain by Paleozoic or younger rocks, and which lies above the shores of the 700-foot post-Glacial lake. They are considerably modified by prairie openings on the youngest surface occupied (the bottom of the 800-foot lake), and to a lesser extent on the next oldest surface (1100-foot lake). They are extremely variable in composition due to the incidence of fire and the admixture of trees induced by fire — jack pine, aspen, and balsam poplar.

Forests of jack pine are most highly developed over the pre-Cambrian rocks on both sides of Lake Athabaska and northward throughout the Tazin and Taltson drainage basins. They extend over the islands in the western half of the east arm of Great Slave Lake and along the eastern shore of the north arm. They are very common on sandy soils throughout the Alberta Plateau, but here they are obviously fire-induced. In the pre-Cambrian country there is considerable evidence that they are not dependent entirely upon fire. Most of them are on surfaces exposed at the drainage of the 1100-foot and 800-foot lakes, and at the retreat of the ice fronts which impounded them.

Balsam fir appears as a primary constituent of our forests only on local flood plains along the Clearwater and lower Athabaska Rivers. The underlying rocks here are Devonian limestones and bituminous Cretaceous sandstones, and the surfaces are probably of about the same age as the 1100-foot lake bottom west of the Slave River. The actual soils, however, are quite recently formed on active flood plains, so that they are perhaps more nearly equivalent to those of the Mackenzie Lowland.

Forests of black spruce and lodgepole pine are known only on uplands based upon Cretaceous rocks in the Caribou Mountain Plateau. These surfaces are also the highest and oldest in the region. Parts of them were not only above the shores of the 1600-foot post-Glacial lake, but also they probably stood out above still higher lakes that existed in the upper Peace River region and may not have been covered by the ice itself. Similar forests are to be expected on the Birch Mountains and on other plateaus of equivalent history.

Muskeg forest of black spruce and larch is widely distributed in all parts of the region without regard to surface age. The large number of undrained depressions in the Laurentian country makes for a somewhat larger development of muskeg there than elsewhere.

Both consistencies and inconsistencies are brought out by this comparison of forest geography with the distribution of geological formations and surface ages. The northeastern limit of the pine forests is nearly coincident with an age boundary, while its southwestern limits are roughly those of the pre-Cambrian rocks. The upland mesophytic forests are bounded approximately by the borders of the 700-foot post-Glacial lake, and the flood plain spruce is clearly correlated with the Mackenzie lowland. Most of the park-like spruce woods are on the most recently exposed surfaces in the pre-Cambrian region.

Both the jack pine and the park-like spruce types, on the other hand, present some anomalies. The pine occupies land of approximately the same age as the upland white spruce. It is very common, of course, in the spruce country, but chiefly as a fire tree. Is this difference to be attributed entirely to the slow development of soils in the pre-Cambrian area, or are there factors of climate and species history to be considered? The presence of park-like spruce on stony and sandy beaches around Lake Athabaska is likewise anomalous. There can hardly be enough difference in surface age to account for the sharp limitation of the spruce to one or two ridges on the lake shores, or to a series of higher beach ridges composed of stones from the Athabaska and Beaverlodge Series of rocks, or to narrow strips on the windward margins of sand blowouts. Also, why should this forest appear on the tops of high sand ridges in the Alberta Plateau west of the Slave River? Here again factors of climate and species history may be effective.

Correlation with Climatic Zones of Vegetation

Comparison of actual climatic zones with the preceding maps is impossible with present knowledge, but there are certain outstanding facts in the zonal distribution of vegetation in the subarctic that are applicable. It has long been assumed that the Arctic, Hudsonian, and Canadian zones of

plant and animal life are climatic phenomena, although the demonstration of the limiting climatic factors which determine the boundaries in our region is difficult or impossible. This is particularly true since one of these boundaries is so nearly coincident with the margin of the crystalline pre-Cambrian rocks, and since an intermediate boundary, between jack pine and park-like spruce types, may be related to one of surface age. Nevertheless, as has been shown above, there are climatic gradients in the region which probably radiate from the tundra country at the northeast.

Halliday (1937) has attempted to extend Thornthwaite's classification of North American climates (1931) into northern Canada and to correlate it with his forest sections. His figures are of necessity, however, based upon so few observational data for our region that they are of very doubtful significance. For all of his "Northern Transition Section," for instance, he draws data from only one station, and for his "Northern Coniferous Section" he has no data at all.

An investigation of the root habits of northern trees by H. E. Pulling (1918) lends significance to climatic factors as they are expressed in terms of soil frost. A classification of the common trees on the basis of the relative flexibility of their root habits suggests a measure of their success in coping with permanently frozen subsoils. White spruce, with a shallow flexible root habit, is most successful, and extends far out into the tundra in favored places. Other shallow-rooted species which have a rather inflexible system, such as white birch, larch, and black spruce, also have a wide range in the subarctic, but are not quite so frost-tolerant as the white spruce. Jack pine has a deep inflexible taproot which requires soils in which the level of permanent frost is low. If this hypothesis is tenable there should be concentric zones of white spruce followed by jack pine around the borders of the tundra, much as we have them now.

The northern limit of trees is an irregular line extending in a northwest-southeast direction through the Lockhart basin, and passing to the northeast of Great Bear Lake. The more mesophytic forests at and just south of the timberline are of white spruce in comparatively open stands, in park-like arrangements on sand and gravel plains or in crevices. Flood plains also have a timber of white spruce, though it is smaller and more open that the flood plain timber of the Mackenzie lowland. Muskeg habitats, of course, develop black spruce and larch. This is the "Northern Transition Section" in Halliday's classification of Canadian forests (1937), and it is essentially the "park-like white spruce" of the Athabaska–Great Slave Lake region (map, *Fig. 5; Plates 1, 2*).

Southwestward in the pre-Cambrian region the white spruce is largely replaced by jack pine, in a belt extending northwestward beyond the north arm of Great Slave Lake (*Plates 3, 4*). This forest is the "Northern Coniferous Section" of Halliday, extending from near Great Slave Lake southeastward across northern Saskatchewan, central Manitoba, and far into western Ontario. According to Halliday it is broken only by a somewhat more mesophytic type in the Nelson River area. In our region it can be extended farther northwestward than Halliday has it.

The pine and white spruce types together occupy the "Hudsonian Life Zone" of Merriam (See Preble, 1908; Harper, 1931–A; Anderson, R. M., 1937–A, B; Porsild, 1937). They are bounded at the southwest and south by the "Canadian Zone," characterized by more mesophytic coniferous forests of white spruce or mixtures of balsam fir and white spruce. Upland elements of such forests, much altered by fire, are classed by Halliday in his "Mixedwood Section." They correspond in general to the upland meso-phytic spruce forests of the preceding discussions. Their eastern boundary in the Slave River region should extend nearer the river than Halliday has placed it. Most of the flood plain elements are classed by Halliday in the "Mackenzie Lowlands Section," and probably correspond to our flood plain white spruce type.

The faunal boundary between the Hudsonian and Canadian Zones in our region appears to be somewhat in doubt. Preble placed it at the valley of the Slave River, but Harper has proposed that it be put farther east-ward, on a line extending roughly from the south shore of Great Slave Lake not far east of the Slave River to Hill Island and Tazin Lakes, thence to the Beaver River near the eastern end of Lake Athabaska. Harper relates the triangular area bounded by this line and by the Slave River and Lake Athabaska to the Canadian Zone. However, he regards it as sufficiently different faunally to set it up as a separate faunal area designated by the name "Tazin Highlands."

With the amelioration of climates and the development of forests after the ice sheet and glacial lakes receded, forest successions must have been initiated. We have already seen that the first two stages on the better drained soils were probably park-like white spruce followed by jack pine, both of which are still abundantly represented. The pine should, in turn, have been followed by another zone of spruce that should have developed as the forest became more mesophytic. That is, under more equable climates heavier stands of timber would appear, with accompanying humus accumulation and the improvement of soils. There is considerable evi-dence that this succession from pine to spruce has occurred in the region in the "Canadian Zone" west of the Slave River, and that in some places it is not yet complete (Raup, 1935, pp. 23–26). Low sand ridges that have only recently been exposed by the drainage of morainically dammed lakes develop an initial forest of jack pine. In sand plains throughout this area the permanent frost is far below the surface; and when they are so severely burned that all humus is removed, they invariably begin their revegetation with pure stands of jack pine. The pine, however, is not permanent, but is followed directly by white spruce. Stages in this succes-sion are common on sandy uplands in the Wood Buffalo Park.

Further stages in the increase of mesophytism require time for the further development of soils. They would be hastened by an improvement in climate, particularly by more rainfall. In our region the principal evidence of a later stage is to be found on the Cretaceous surfaces in the south, where many plants of rich woods reach their northern limits, and

where the balsam fir shares with white spruce the primary situation in the forests of the flood plains. These surfaces are older than those of the Wood Buffalo Park and enjoy a somewhat greater rainfall during the growing season.

Given a uniform distribution of soils throughout the Athabaska–Great Slave Lake region, and no great differences in the age of its surfaces, a group of concentric forest zones such as have just been outlined might be expected on the basis of climate and successional development alone, with boundaries more or less parallel to the arctic timber line. The Paleozoic-pre-Cambrian boundary, however, with its effects upon glacial deposits, has accentuated the jack pine stage. The sterility and scarcity of soils in the pre-Cambrian area seem to have retarded the development of more meso-phytic spruce forests, so that the southwestern boundary of the pine becomes locally an edaphic one. At the northeastern margin the correlation with surface age may be more apparent than real, since we know very little about the actual configuration of the transition from park-like spruce to pine. Studies of permanent frost levels in that region would be of great interest. A faunal reflection of a "lag" in the development of more meso-phytic forests east of the Slave River may be found in Harper's delineation of a "partially" developed Canadian Zone fauna in his Tazin Highlands area.

There is still the anomalous appearance of park-like spruce at Lake Athabaska and on the Alberta Plateau to be dealt with (map, *Fig. 5; Plates 1, 2*). When I discussed this in an earlier paper (1933) I came to the tentative conclusion that the southern outliers of the open spruce were "relics," persisting on sites which the pines had been unable to invade. Excessive exposure to storm winds seemed the only common limiting factor among the situations examined up to that time. The gradual transition at Sand Point from an old forest of open white spruce, on the outer part, to one of old pines, and then to one of younger more closely grown pines at the base of the point seemed particularly strong evidence that exposure to strong winds off the lake was significant.

Further observations around Lake Athabaska have cast some doubt that this is a sufficient cause in all cases. The spruce was found on ancient stony beaches high above the lake at Charlot Point where it is more or less protected from strong northeast and northwest gales; and it likewise occurs on hills of conglomerate and dolomite in the Charlot Point and Beaver-lodge districts where it is not unduly exposed. It may be that extreme xerophytism or instability of the soils may be effective as well as storm winds. In all the areas studied to date both of these factors are present. The conglomerate and dolomite are weathering to form soils that are on steep slopes and subject to frost heaving and creep. The ancient stony beaches are excessively dry, with almost no water-holding capacity at all. All of these habitats may present difficulties which are insurmountable to the invading jack pine. In any case it still seems most reasonable to con-sider the southern outliers of park-like spruce as relics of a former wide-

spread forest of this type, particularly in view of the possibility that the whole of the pre-Cambrian jack pine region has been held back in its successional development by poor edaphic conditions. Further reason for holding to this view is to be found in the Glacial and post-Glacial history of the species, and in their probable routes of migration into the region (see below.)

The following is a provisional scheme for the post-Glacial development of forests in our region, taking into account the progressively younger surface ages (*Fig. 6*). It also involves a progressive amelioration of climates

FIG. 6. Provisional outline for the development of forests in the Athabaska–Great Slave Lake region since the retreat of the last Pleistocene glacier and the post-Glacial lakes.

during the retreat of the ice and the drainage of the post-Glacial lakes. It will be noted that I have inserted, tentatively, a park-like spruce stage following tundra in most of the successions, although this is now most evident in the Laurentian province. The occurrence of suspected relics of such a forest on the Alberta Plateau west of the Slave River and the present existence of it on Cretaceous sedimentary rocks northwest of Great Bear Lake (Porsild, 1937) strongly suggest that it occurred over Paleozoic and younger rocks as well as over pre-Cambrian formations. Whether or not tundra was the original vegetation on the clayey soils of the 1100-foot and 800-foot lake bottoms is conjectural (Raup, 1934, pp. 94–105; 1935, pp. 60–61; 1941, pp. 219–21). On the most recent

surfaces it may well have started as a grass-sedge tundra that was closely related to prairie.

Stages leading to the black spruce–lodgepole pine forest on the high plateau of the Caribou Mountains are also problematical. It is not improbable that tundra and simple white spruce forest constituted the initial stages at least on the lighter soils, but on heavier soils it may be that tundra persisted for a very long time, perhaps prairie-like in its later aspects. Similar forest on the high plateaus between Fort St. John and Nelson and in the upper Liard region gives some evidence of recent development, possibly from some form of tundra or grassland (Raup, 1945, pp. 40–42).

The timing of events presented in the diagram is undoubtedly subject to modification. We have no way of knowing, for instance, how long it took the tundra on the 1100-foot lake bottom in the crystalline area to develop an open spruce forest on its river bottoms and sand plains, and finally on its rocky uplands. This tundra may have lasted until after the drainage of the 700-foot lake when all the ice disappeared from the Slave Lake basin, rather than to the drainage of the 800-foot lake as I have it. Furthermore, the whole scheme is based upon an amelioration of the climate during which there may have been halts, but no important reverses.

The question is not solved as to whether the central Mackenzie basin has experienced a post-Glacial climate that was milder than that of the present. The evidence for such a climate in the Athabaska–Great Slave Lake region is scanty and equivocal.

A rather imposing body of research in other parts of North America and Greenland, as well as in the Old World, gives strong indication that many of the northern parts of the earth have undergone a "deterioration" of their climates during the past 3000 to 7000 years. It is unnecessary to review this research in detail, for several comprehensive statements of it have been published recently (Cooper, 1942; Cain, 1939; Sears, 1935; Raup, 1941; Bull. Am. Meteorolog. Soc., 1938). The evidence is drawn from many fields: the advance and retreat of modern Alaskan and other Cordilleran glaciers, conditions at arctic and alpine timberlines, the present distribution of temperate and arctic biota, the history of peat deposits as shown by their gross morphology and fossil pollens, ancient dune deposits in the upper Mississippi valley, the history of saline lakes in the Great Basin, geothermal gradients in deep mines, and the migrations and cultures of ancient peoples.

The presence of semi-open prairies in our region might suggest a warmer or drier climate during which they could have acquired their present expansion. Nevertheless there is no evidence whatever that the present sites of the prairies ever had any other vegetation than grassland or some form of tundra. The prairie soils give no indication of ever having had forest on them.

The timber line seems to be advancing in parts of Alaska (Griggs, 1934–A, B), while it has retreated a little in the lower Mackenzie and

Coppermine regions (Porsild, 1938; Richardson, 1851). On the other hand Clarke (1940) thinks that it has been approximately stable for a long period in the upper Thelon country and the Lockhart basin east of Great Slave Lake; and J. B. Tyrrell (1910–A) could find no evidence in the region southwest of Hudson Bay that the forests had ever extended farther north than they do now.

The effects of a previously warmer climate in the Athabaska–Great Slave Lake region might be looked for also in isolated northern relics of southern floristic elements. To draw any conclusions from the few apparent range discontinuities now known, however, is extremely hazardous because of the incomplete exploration of the country. In fact, the number of these cases is so small, and their validity is so doubtful, that the most reasonable conclusion at present is that they give little or no indication of a change in climate. An example is the balsam fir, *Abies balsamea*. Its authenticated northern limit is the Athabaska delta, but it was reported by Richardson at latitude 62° on the Mackenzie. No specimens to substantiate Richardson's record appear to be extant, and no one has ever been able to verify the observation. There is, however, a northwestern variety of the white spruce along the Mackenzie in latitude 62° which has the smooth, resin-blistered bark of the fir and would easily be confused with it. Another instance is that of *Trillium cernuum* var. *macranthum,* a specimen of which in the Gray Herbarium is labeled "Mackenzie River." The plant was collected by Richardson and is the only specimen of *Trillium* ever credited to any part of the Mackenzie basin.

In the region of the Mackenzie delta Porsild (1938) has found abundant evidence of a former northern extension of the forest amounting to at least 50 or 60 miles. In the Eskimo Lakes basin he found what he considered to be isolated representatives of several herbaceous plants. Some of these, however, have already been found in the upper or middle Mackenzie country, so that their range discontinuities are somewhat in doubt.

Reasons for the failure to find evidence of a post-Glacial "optimum" climate in our region can only be conjectured. It is not impossible that a general cooling of climates throughout the northwest, with an attendant increase in precipitation in some places (or perhaps an increase in storminess), would allow a continued advance of forests under the relatively equable marine climates of coastal southern and western Alaska, but would have quite dissimilar effects in the continental interior. Under the latter climates, where temperature is more likely to be a controlling influence (see Thornthwaite, 1931), even an opposite effect might be produced, and the northern forest border would retreat as it seems to have done in the Mackenzie delta and the Coppermine region. If this should prove to be the case, it would be possible to postulate a region in which effects of changes in temperature and precipitation would offset each other, and timberlines would remain relatively stable for a long period in spite of a general "deterioration" of climates. The arctic limits of timber south and west of Hudson Bay, thought to have remained nearly stationary for a long time, might be explained in this way.

Giddings, in his studies of Alaskan dendrochronology (1941), found a close correlation between temperature phenomena and tree growth at altitude and latitude timberlines in central and northern Alaska. At the same time he could find no apparent correlation with differences in precipitation in those regions. Climatic correlations with growth in lowland trees were not so clear, though Giddings says that "even here temperature seems more to be considered than does any particular precipitation or ice effect."

If the hypotheses concerning climatic controls just outlined are tenable, disrupted ranges due to deteriorating climates would not be any more probable than migrations of the timberline in the Athabaska–Great Slave Lake region.

Another reason for the failure to find evidence of a more equable climate in our region might be that the establishment of forests there was achieved coincident with the climatic "optimum." It would be entirely possible for the forests to maintain their status or even to spread during a subsequent period of general deterioration provided the interplay of climatic factors has produced for a long time a fairly constant effect similar to that now obtaining. Continued development toward mesophytism would of necessity be slow and would be accompanied by a retarded development in soils. The present immaturity of both vegetation and soils lends some weight to this theory.

Antevs (1931) has estimated that glacial ice still remained somewhere in Keewatin and in the Labrador Peninsula as late as 7500–9000 years ago, to the close of his "Younger Late-Glacial." One of the later stages in the shrinkage of the remnant in Keewatin may well have been that which finally cleared Great Slave Lake of ice and brought the lake nearly to its modern level. As will be shown below, there is evidence that extensive forests did not come into the Athabaska–Great Slave Lake region until after the ice had left Great Slave Lake. Antevs (1935) places the post-Glacial warm period between 7000 and 4000 years ago, but quotes Spitaler (1932–A, B) to the effect that the maximum summer temperatures may have been reached about 8500 years ago. The final disappearance of ice from Keewatin, therefore, may have fallen within the period of the post-Glacial optimum, and the establishment of forests in our region might also have been coincident with it. All of these figures, however, are highly conjectural, especially since relations between the recessional moraines in our region and those studied by Antevs in Ontario and Manitoba are not known.

In any event, much more study is needed before any conclusions can be reached. It should be particularly useful to make a thorough investigation of peat deposits from the oldest to the youngest surfaces, using the methods not only of pollen analysis but also of macroscopic examination. This appears to present an entirely open field of research in our region. Above all, correlations should be made between the lake stages and morainic systems in our region and those of the southern prairie provinces and Ontario.

CORRELATION WITH THE GLACIAL AND POST-GLACIAL HISTORY OF THE SPECIES

Some recent studies by Hultén (1937) on the origin and distribution of boreal plants in Pleistocene and post-Pleistocene time have made it possible at least to postulate origins for the tree populations now found in the Athabaska–Great Slave Lake region. Still more recently, Halliday and Brown (1943), using Hultén's hypotheses, have attempted to outline the post-Glacial migrations of the principal forest trees of Canada. The essential ideas involved in Hultén's study have already been discussed at length elsewhere (Halliday and Brown, ibid.; Raup, 1941; Stebbins, 1942) and need not be described here.

Pairs of closely related species have long been recognized in eastern and western America: *Abies balsamea* and *A. lasiocarpa, Pinus Banksiana* and *P. contorta, Tsuga canadensis* and *T. heterophylla, Thuja occidentalis* and *T. plicata,* etc. To these may be added eastern and western varieties within single species: *Picea glauca* and its var. *albertiana, Betula papyrifera* and its vars. *commutata* and *neoalaskana, Larix laricina* and its var. *alaskana* (see Hultén, 1941). It is presumed that these pairs date from pre-Wisconsin time, when they existed in the east and west as geographically separate entities or as geographic varieties in species whose continuous populations stretched across the continent. It is thought that in the latter case the connecting elements were destroyed by the advancing ice sheets, and in either case the eastern and western segregates were kept apart until after the retreat of the glaciers. The rates at which representatives of the pairs have moved into the interior subarctic plain of the continent since the retreat of glacial and glacio-lacustrine conditions should depend upon their requirements as to mesophytism, the progressive availability of lands and climates, and, following Hultén's hypothesis, upon the success with which they maintained their spreading capacity, with large populations and large numbers of biotypes, during the Late Wisconsin period.

The principal refugia for Canadian forest trees during the Late Wisconsin ice advance are thought to have been south of the ice in the western Great Lakes region and the northern Appalachians, on the exposed continental shelf off eastern Canada and the northeastern states, a western continental area centering in the upper Yukon valley or in the mountains south of it, a north Pacific coastal area, and possibly a lower Yukon or Bering Sea area. Of these refugia the ones most likely to have made large and early contributions to the flora of the Athabaska–Great Slave Lake district were in the Great Lakes region, and in the northern Rocky Mountains and the upper Yukon. Later contributions could be expected from more mesophytic elements in both these areas or from more distant ones such as the eastern continental shelf, and to a lesser extent from the Pacific areas.

A scale of mesophytism may be drawn up on the basis of the present distribution of the trees, using also for the more northern species Pulling's scale of adaptability in root habit. The least mesophytic group among the trees in our region would include the white spruce, larch, black spruce, white birch, and possibly aspen. Next would be jack pine, lodgepole pine, and balsam poplar, and finally would come the balsam fir.

Hultén, and later Halliday and Brown, have set up a scale of success among these trees in maintaining genetic variability during the Wisconsin period. All of the species are boreal in their general distribution, and it might be expected that with the progressive destruction of their normal habitats and ranges, the more mesophytic ones would suffer the greatest reduction, while those more tolerant of varied boreal conditions would suffer least. Halliday and Brown suggest that the white and black spruces had ample refugia south of the ice, consequently maintaining large genetic variability and extensive ability to migrate. The same may be said of the aspens and poplars, and possibly also of the birches and larches. The jack pines are thought to have had their refuge in the western Great Lakes region, where they were more or less restricted in space; while the lodge-pole pine was restricted to relatively small refugia in the northern Cordil-lera. The balsam fir is thought to have been restricted to the continental shelf off northeastern America, and to limited areas south of the ice.

The white spruce consists of at least two geographic races or varieties in the region south and west of Hudson Bay. Throughout Quebec and Ontario is typical *Picea glauca*, a tall tree of broadly pyramidal form. In Keewatin, Mackenzie, northern Alberta, and northern Saskatchewan the white spruces are narrowly pyramidal or columnar in form, and represent the so-called "Alberta spruce," *Picea glauca* var. *albertiana*. This is the commonest white spruce also in the northern Rockies and in Yukon and Alaska. Trees intermediate in form between these two are seen in the southern and southwestern parts of our region; and in the Athabaska–Peace delta there are trees that could be called typical white spruce (*Plate 2*). The narrowly pyramidal habit is most accentuated in the park-like spruce type (*Plates 1, 2*).

The larches around Great Slave and Athabaska Lakes prove to be closely related to, if not identical with, the so-called Alaska larch, and it is pre-sumed that there is a transition to the eastern form in this region and southeastward. The Alaska larch, however, has never been widely recog-nized among botanists, and no specimens of any kind of larch are available from the southern part of our area. Consequently the geography of these forms can at present only be conjectured.

Most of the white birches in our region are *Betula papyrifera* var. *neo-alaskana*, which has its principal range from here northwestward through Alaska. Authentic *B. papyrifera* var. *commutata*, the other western variety, has been found at Lake Athabaska. The typical eastern form of the white birch extends scarcely beyond the lower Athabaska River, where it mingles with these western varieties.

Among the aspens there is a rather poorly defined Cordilleran phase called *Populus tremuloides* var. *aurea*, distinguished chiefly by the fact that its leaves turn golden yellow in the autumn. This is the common form in the upper Mackenzie valley and around Great Slave Lake, but in the central and southern parts of our region there appears to be a gradual transition to the eastern forms in which the yellow color is not marked. So far as is known at present the balsam poplars are not divisible

into eastern and western races, though it is possible that such will appear upon further study.

The jack and lodgepole pines, more southern in their general distribution, have only slightly overlapped their ranges. They appear to merge in central and western Alberta, and possibly also in the lower Liard River region (see Halliday and Brown, ibid., *Fig. 4*).

The eastern and western firs, *Abies balsamea* and *A. lasiocarpa,* have not joined their ranges at all, although they apparently have come near to doing so in central Alberta. Other still more southern pairs such as the hemlocks and arborvitaes are yet far apart, and are not represented at all in the northern interior plains.

The most widespread species complexes in our forests are the spruces, larches, birches, and aspens. Also it is this group that stands lowest in the scale of mesophytism and highest in the scale of suspected ability to migrate and cope successfully with subarctic conditions. Further, they are the species that have most thoroughly merged their eastern and western racial components. The firs, on the other hand, are the most mesophytic trees we have, and among the most restricted, geographically, in our region. They are also low in the scale of suspected ability to migrate, and have not joined their eastern and western components since the retreat of the glaciers. The pines are intermediate in mesophytism and in the extent of their present northern ranges. Likewise they have been only moderately successful at merging their eastern and western types. The balsam poplars, judging by their present range, probably are to be classed with the pines in this arrangement. Halliday and Brown, however, place them among the species with the greatest spreading capacity.

The above notes suggest further that the more northerly parts of the Athabaska–Great Slave Lake region have the stronger representation of northern Cordilleran and Yukon elements in their forests. These elements are accentuated in the park-like spruce type, wherein the western varieties of the white spruce, larch, white birch, and aspen are least "contaminated" by eastern strains. The same relationship is to be seen in other parts of the flora. The following is a list of species found around the large lakes but not thus far in the Cretaceous uplands farther south.

> *Woodsia oregana, Woodsia scopulina,*[16] *Poa lanata, Deschampsia mackenzieana, Cyripedium guttatum, Salix MacCalliana, Salix Farrae, Arenaria macrophylla, Sorbus scopulina, Dryas Drummondii, Epilobium leptocarpum* var. *Macounii, Chimaphila umbellata* var. *occidentalis, Arctostaphylos Uva-ursi* var. *adenotricha, Trientalis europaea* var. *arctica, Pedicularis parviflora, Boschniakia rossica, Aster sibiricus,*[17] *Antennaria pulcherrima.*

It should be noted also that the black spruce–lodgepole pine forest of the foothills of the northern Rockies (see Halliday, 1937; Raup, 1945) has

[16] A few of these species have isolated stations in the Great Lakes or Gulf of St. Lawrence regions (see Fernald, 1925).

[17] *Aster Richardsonii* of the Catalogue. See Porsild in Rhod. 41: 291. 1939; Scamman in Rhod. 42: 339. 1940; Hultén, Fl. Kamtch. 4: 157–158. 1927–30, and Fl. Aleut. Isl. 317–318. 1937.

its longest range extension into the west central part of our region rather than into the southern part.

At the same time the more southern and eastern affinities of the vegetation of the lower Athabaska district are substantiated by the presence of species which, like the balsam fir and the eastern white birch, are at or near their northern limits in this vicinity.

> *Dryopteris spinulosa, Pteretis nodulosa, Lycopodium obscurum* var. *dendroideum, Cinna latifolia, Carex Deweyana, Disporum trachycarpum, Lilium philadelphicum* var. *andinum, Corylus cornuta, Anemone cylindrica, Coptis groenlandica, Prunus demissa, Glycyrrhiza lepidota, Rhamnus alnifolia, Pyrola elliptica, Trientalis borealis, Agastache Foeniculum, Galium triflorum, Xanthium italicum, Helianthus giganteus.*

Many more species could be added to this list, but these will serve to characterize the group.

Evidence presented earlier suggests that the initial post-Pleistocene forests in our region were of park-like white spruce, with black spruce and larch in the muskegs. It is now possible to suggest that these forests came into the area from the west or southwest, and that descendants of the initial populations still persist in the pre-Cambrian region (*Fig. 6*). They are more or less isolated there by the zone of jack pine which has been accentuated and retarded in its development toward mesophytism by the scarcity and sterility of the soils. In the light of these suggestions it is reasonable to expect that in our three types of white spruce forests we are dealing with two or possibly three genetic strains within the species. Factors determining the present distribution and structure of the types, therefore, may have to include elements not only of climate, soil, and age of surface (time), but also of the inherent migratory capacities of the genetic strains that make up the populations.

One of the corollaries of the genetic theory as applied to geographic problems is that when two or more separate but closely related populations regain their continuity they acquire increased spreading capacity by the interchange and recombination of biotype material. If this can be applied to the white spruce forests in our region, then the park-like type should have somewhat less ability to colonize than the upland mesophytic and lowland types in which the eastern and western strains seem to have been combined (see *Fig. 6*).

The question naturally arises whether we have also more than one strain of jack pine. The pines that came early into the pre-Cambrian country could have been derived from a limited glacial population which would later have been merged with others to form a more aggressive type. It is not impossible that the pines of the Tazin and Taltson basin, for instance, are descendants from the early immigrants, while the "fire trees" of the Alberta Plateau are later invaders.

It will be noted from preceding discussions and from the diagram in *Fig. 6* that the earliest possible dates for the initiation of forests in the Athabaska–Great Slave Lake region were set by the progressive exposure of the land surfaces. The timing of events during the invasion by forests must have been conditioned by the availability of populations of trees in

the areas immediately south and west of the retreating lakes and glaciers. This raises, in turn, the question of whether there was an interglacial vegetation between the Tazewell–Carey (W_2) and the Altamont or Mankato (W_3) glacial substages in western Canada, and of whether this vegetation could have persisted there through Late Wisconsin (W_3) time.

During Late Wisconsin time there must have been a large, roughly triangular area in Alberta and southwestern Saskatchewan that was free of ice. Its western border was at the Cordilleran glacier and its northeastern margin was approximately at the position of the ice front which finally built the Altamont moraine. Presumably its northern angle was somewhere in the upper Mackenzie valley. Its surface must have been broken by the remains of glacial lakes, and by glacial streams swollen with melt water and loaded with detritus (see Bretz, 1943). Drainage was probably southward to the Missouri. As the ice receded northeastward new lakes were formed at its border, among them those in the Athabaska and Peace River valleys. Outlets for the latter must have shifted first to the Saskatchewan, and possibly later to the Churchill.

One of the outstanding characteristics of the modern deltas and flood plains of the Athabaska, Peace and Hay Rivers is the immense amount of vegetable detritus that is being laid down in their alluvial silts. Lake Athabaska receives most of the material brought down by the Athabaska River, and it also receives a considerable quantity from the Peace. Most of the latter, however, is carried on down the Slave River and deposited on the southern shore of Great Slave Lake. Since the drainage of the last of the post-Glacial lakes these streams have nearly filled a huge western extension of Lake Athabaska, leaving only the shallow, weed-filled Lakes Claire and Mamawi. At the same time the Peace and Slave, aided at times of unusually high water by the Athabaska, have filled a great southern arm of Great Slave Lake. Driftwood, much of it in the form of large logs carried from the whole forested watershed of these rivers, is concentrated in the lower flood plains and deltas. The streams meander about in their broad valleys, shifting their channels frequently, depositing here and undercutting there. Undercut banks show thick layers of mud embedding tangles of drift timber. Spring floods often lodge mountainous piles of logs in channels that are abandoned later in the season.

The outer parts of the deltas are mud flats thickly scattered with partially buried logs. Much timber, however, finds its way into the open lakes where it is blown about by winds or carried by currents to be washed up on the beaches. At Lake Athabaska great "windrows" of such drift are common on the beaches forty to fifty miles east of the river delta, while at Great Slave Lake they line the southern shores. The Slave River leaves practically all of its load in Great Slave Lake, for the water is clear when it enters the Mackenzie.

It is of interest to note that evidence of this type of alluvial deposit has not been seen in the Mackenzie basin except in the more recently formed flood plains and deltas. If it had been developed at any of the

higher lake stages, remains of it should have come to light in the dissected beds of these lakes as they are exposed in the main river valleys. Such of the older lacustrine deposits as may be interpreted as deltas are mostly of stratified sand and gravel, and contain no logs.

Around the larger lakes only the lowermost of the old beaches contain driftwood. If the earlier lakes had received any quantity of logs, some of the latter should have been embedded in the higher ancient beaches, just as the modern drift is being lodged in the current shore deposits.

A question can be raised as to the likelihood of the preservation of driftwood in the ancient deltas and beaches. There is no reason to believe that conditions here are less suitable for the preservation of vegetable remains than they are in places where interglacial forest beds have been found (see Wickenden, 1931; Wilson, 1932, 1936). Such beds are found associated not only with peat deposits, but also with glacial outwash and till. In fact preservation might be better in the colder climates of the north, where bacterial decay is exceedingly slow. Furthermore, if beds of logs had ever been present in the ancient deltas and beaches, evidence of them would still remain in the distortion and discoloration of the strata. The older deposits show neither of these effects.

The preceding observations indicate that the Peace, Athabaska, and their tributaries were not flowing through a timbered country until after the last ice had disappeared from Athabaska and Great Slave Lakes, and until after the lakes had nearly reached their present levels. They indicate further that, during late Wisconsin time, at least the northern part of the unglaciated area of Alberta had no forests of any consequence, and must have been under some form of tundra. Consequently, for all but the lowest of the old lake bottom surfaces in our region, there must have been a time interval of some length during which tundra persisted.

It is significant that the lacustrine deposits in Lake Agassiz, as well as those in the Souris basin, received driftwood only in the latest stages when most of the bottom of Lake Agassiz was finally exposed. Upham recognized the difference in kind between the sediments of the ancient lake and those of the recent alluvium. He stated it clearly as follows (1895, pp. 201–202): "After the drainage of the glacial lakes by the complete departure of the ice-sheet, the lower portions of their basins, in depressions and along the present river courses, have become filled to a considerable extent by fluvial beds of fine silt. These are similar in material with the lacustrine sediments bordering the deltas, from which they are distinguished by their containing in some places shells like those now living in the shallow lakes and streams of the region, remains of rushes and sedges and peaty deposits, and occasionally branches and logs of wood, such as are floated down by streams in their stages of flood." Again (l. c., pp. 253–254) he says, "Thus the occurrence of shells, rushes, and sedges in these alluvial beds at McCauleyville, Minn., 32 and 45 feet below the surface, or about 7 and 20 feet below the level of the Red River, of sheets of turf, many fragments of decaying wood, and a log a foot in

diameter at Glyndon, Minn., 13 to 35 feet below the surface, and numerous other observations of vegetation along the Red River Valley in these beds, demonstrate that Lake Agassiz had been drained away, and that the valley was a land surface subject to overflow by the river at its stages of flood, when these remains were deposited."

The evidence from Lake Agassiz, therefore, strongly suggests that southern Alberta, Saskatchewan, and Manitoba were also devoid of forests during late Wisconsin time and during the retreat of the Mankato ice. They must not have appeared in this region until the ice had left the Lake Agassiz basin, and until after the lake had been drained.

Time relations for Lake Agassiz and the glacial lakes of the Mackenzie basin are not known. If they were contemporaneous, then the arrival of eastern forest elements in the Athabaska–Great Slave Lake region had to await the migration of these trees all the way across Manitoba and Saskatchewan. If Lake Agassiz were drained at an appreciably earlier date, the forests could have moved into southern Saskatchewan and Alberta before the northern lakes reached their lower levels, so that the tundra period for our region could have been proportionately somewhat shorter.

The existence of forest in our area during the interglacial interval between Tazewell-Carey and Mankato time is still a matter for conjecture. So far as I am aware no interglacial deposits of vegetable remains have been described in the Athabaska–Great Slave Lake region nor in the upper Peace and Athabaska River districts. Wickenden (1931) has described interglacial beds in the vicinity of Johnstone Lake in southwestern Saskatchewan. These are in and near the Altamont moraine and lie between two tills, the upper of which is to be regarded as of Mankato origin, and the lower probably of Tazewell-Carey. The beds contain vegetable remains, among them cones, branches, and logs of spruce. Presumably these are to be correlated with the Two Creeks forest bed described by Wilson (1932, 1936) in Wisconsin (See also Wilson, 1938). No species of trees other than spruce were noted by Wickenden at Johnstone Lake. Further discoveries are necessary before it will be known how far northward in the Great Plains the interglacial forests extended, and whether they achieved as great or greater floristic complexity than those now living there.

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Athabaska–Great Slave Lake Region, II
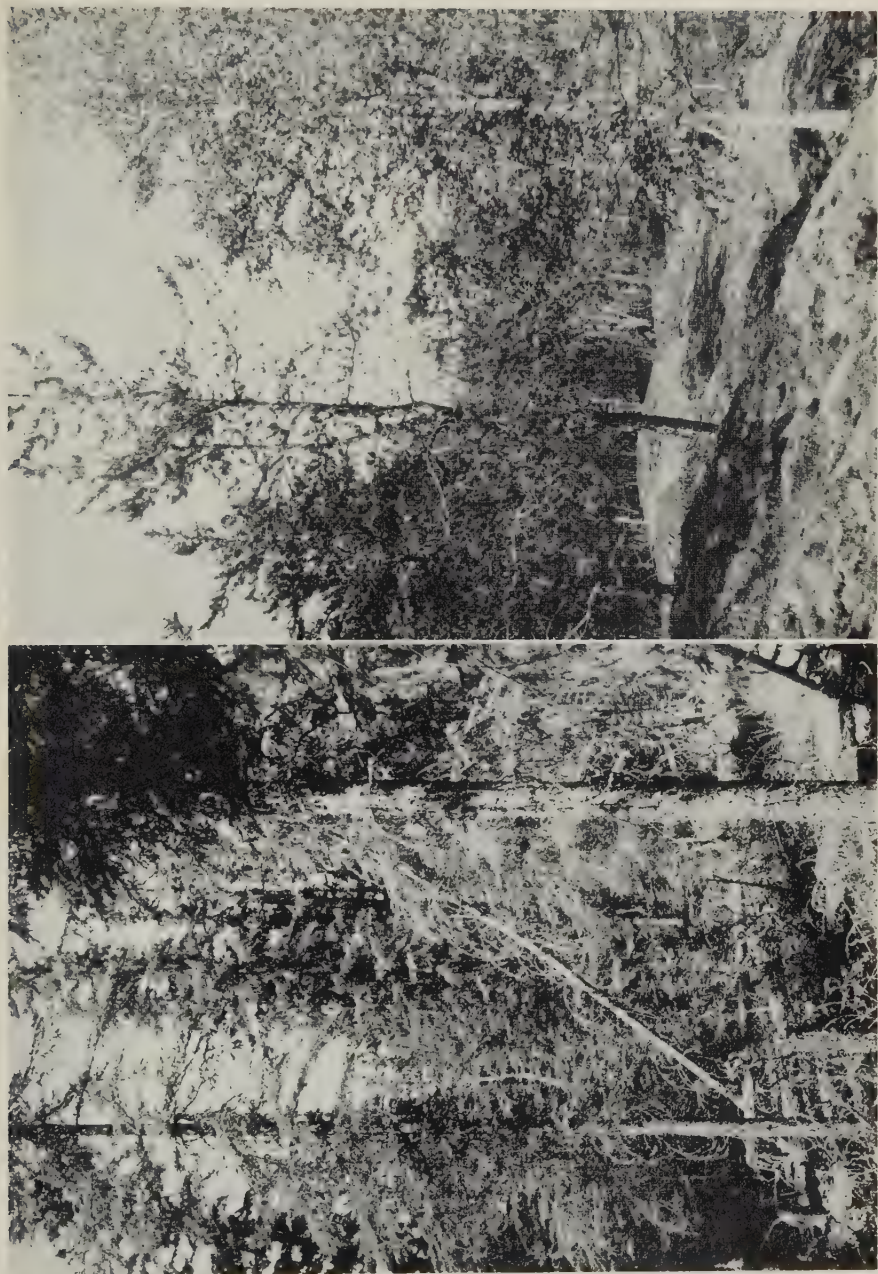
ATHABASKA–GREAT SLAVE LAKE REGION, II

Plate III

Athabaska – Great Slave Lake Region, II

Athabaska–Great Slave Lake Region, II

Plate V

Athabaska–Great Slave Lake Region, II

EXPLANATION OF PLATES

PLATE I

(Upper) Park-like white spruce on ancient stony beaches near lake shore, northwest side of Fairchild Point, Great Slave Lake.

(Lower) Park-like white spruce forest on sandy beach ridges near Ennuyeuse Creek, south shore of Lake Athabaska.

PLATE II

(Upper) Park-like white spruce at western margin of active sand dune area, Wolverine Point, south shore of Lake Athabaska.

(Lower) Flood plain forest of white spruce and occasional balsam fir, upper part of the Athabaska River delta, near head of Embarras Channel.

PLATE III

(Left) Upland mesophytic forest of white spruce on Alberta Plateau near Pine Lake, west of the upper Slave River.

(Right) Jack pine and white birch on granite hill along the upper Slave River.

PLATE IV

(Upper) Open forest of jack pine in sand dune country southwest of William Point, Lake Athabaska. Note young pines.

(Lower) Jack pine forest on sand plain near Wolverine Point, Lake Athabaska.

PLATE V

(Upper) Forest of black spruce in crevices on ledges of Athabaska Sandstone, about 5 miles east of Poplar Point, Lake Athabaska.

(Lower) Muskeg forest of black spruce, Caribou Mountains.

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STUDIES OF SOUTH AMERICAN PLANTS, XI
NOTEWORTHY SPECIES OF HIPPOCRATEACEAE
AND VACCINIACEAE

A. C. Smith

With four text-figures

The present paper is based largely upon material made available to the writer by Mr. E. P. Killip, of the U. S. National Museum, and Dr. José Cuatrecasas, of the Escuela Superior de Agricultura Tropical, Cali, Colombia. I am greatly indebted to these colleagues for forwarding such interesting material for study. The large collections made in western Colombia by Messrs. Killip and Cuatrecasas are of the greatest importance in a study of the flora of that country. As a result of their work on the Pacific coast and slopes, a great number of new species have been discovered and many range-extensions noted. If other families in this region prove as richly represented as the Vacciniaceae, one may suppose that no other part of South America (except possibly the Venezuela–Brazil boundary) offers such fascinating possibilities to future collectors.

Specimens cited in this paper are deposited in the following herbaria: Arnold Arboretum (A), Gray Herbarium (GH), New York Botanical Garden (NY), and U. S. National Herbarium (US).

HIPPOCRATEACEAE

Elachyptera floribunda (Benth.) A. C. Sm. in Brittonia 3: 387. *fig. 3, a–n.* 1940.
  Hippocratea floribunda Benth. Bot. Voy. Sulph. 78. 1844.
  Colombia: El Chocó: Banks of Quebrada Togoromá, in dense tidal forest, *Killip & Cuatrecasas 39138* (A, US); El Valle: Punta Arenas, north shore of Buenaventura Bay, in mangrove swamp, *Killip & Cuatrecasas 38635* (A, US).

Except for the type collection, made by Hinds on Gorgona Island, the cited specimens are the only ones recorded from Colombia. No. *38635* bears mature fruits, which permit an amplification of my description (1. c.). The fruits formerly described and figured by me were from *Schipp 715*, the type collection of *Hippocratea lancifolia* Lundell; these are slightly smaller and proportionately broader than those of no. *38635*, but the essential details are identical.

Mature capsules lanceolate-elliptic, 5.5–7 cm. long, 1.6–2.5 cm. broad, obtuse at apex; seeds 2, the embryoniferous portion coriaceous, lanceolate-ovate, 30–40 mm. long, 11–16 mm. broad, 1.5–2 mm. thick, subacute at apex, rounded at base, the basal wing oblong, coriaceous, 6–9 mm. long, 3–4 mm. broad distally, slightly narrower at base, extended distally into a very narrow flange or inconspicuous ridge along the inner margin of the embryoniferous portion.

Anthodon decussatum R. & P. Fl. Per. 1: 45. *pl. 74, b*. 1798; A. C. Sm. in Brittonia 3: 420. *fig. 8, g–k*. 1940.

Colombia: Santander: Vicinity of Barranca Bermeja, Magdalena Valley, between Sogamoso and Colorado Rivers, alt. 100–500 m., *Haught 1455* (A, US) (flowers white, very fragrant).

Both the genus and the species are here reported from Colombia for the first time. Previously *A. decussatum* has been known from Venezuela, Peru, Bolivia, and Brazil, while a second species of the genus is known from Panama. The Haught specimen was collected in 1934 but was not available when my monograph was prepared.

Tontelea chlorantha sp. nov.   Fig. 1.

Frutex parvus (demum scandens?) praeter inflorescentiam ubique glaber, ramulis gracilibus cinereis teretibus (juventute leviter angulatis) inconspicue lenticellatis; foliis oppositis, petiolis rugulosis canaliculatis 7–10 mm. longis, laminis chartaceis vel subcoriaceis in sicco fusco-olivaceis elliptico-oblongis, (6–) 8–13 cm. longis, (2–) 3–4.5 cm. latis, basi obtusis, apice in acuminem 8–12 mm. longum obtusum abrupte cuspidatis, utrinque interdum nigro-punctatis, costa utrinque prominente, nervis secundariis utrinsecus 6–8 patulis subrectis marginem versus leviter curvatis anastomosantibusque et rete venularum intricato utrinque prominulis; inflorescentiis axillaribus gracilibus praeter petala glabris vel distaliter obscure puberulis, e basi 3–5-ramosis, ramulis thyrsoideo-paniculatis 3–5 cm. longis pseudodichotome divisis; bracteis papyraceis deltoideo-ovatis subacutis 0.5–1 mm. longis, bracteolis similibus sed minoribus; floribus (post anthesin mox caducis) in ramulis ultimis solitariis sub anthesi circiter 4 mm. diametro, pedicellis gracilibus 1.3–1.5 mm. longis; calyce cupuliformi circiter 1.5 mm. diametro, sepalis ovato-deltoideis, 0.4–0.5 mm. longis, 0.6–0.8 mm. latis, apice obtusis, margine obscure erosulis; petalis sub anthesi patulis submembranaceis oblongo-obovatis, 2–2.3 mm. longis, 1.3–1.5 mm. latis, apice rotundatis, extus et margine et intus apicem versus copiose (sed minute) papilloso-puberulis; disco tenuiter carnoso suberecto, 1–1.2 mm. diametro, 0.3–0.5 mm. alto, apice in lobos parvos 3 inter stamina undulato; staminibus suberectis, filamentis anguste ligulatis circiter 0.7 mm. longis, antheris transverse ellipsoideis circiter 0.2 × 0.35 mm. extrorse dehiscentibus; ovario subimmerso, ovulis in quoque loculo 2 oblique superpositis, stylo cylindrico circiter 0.5 mm. longo, stigmatibus 3 staminibus alternatis conspicue bilobatis, lobis angustis linearibus circiter 0.1 mm. longis patentibus.

Colombia: Vaupés: Yuruparí, Río Vaupés, *Cuatrecasas 7312A* (type, Herbario Nacional Colombiano, Bogotá), Oct. 25, 1939 (arbolillo; flor verde pálido).

A member of the species-group *Laxiflorae,* according to my treatment of the genus in Brittonia 3: 463–502. 1940, *T. chlorantha* is closely allied only to *T. corymbosa* (Huber) A. C. Sm., of Amazonian Peru. From this, the new species differs in having leaves with the secondary nerves less conspicuous and less strongly curved, the petals copiously papillose-puberulent without, and the stigmatic lobes more distinctly separate and spreading. In *T. corymbosa* the stigmas, although conspicuously bilobed, have the lobes clearly united in pairs (A. C. Sm. in op. cit. *fig. 10, m*); in *T. chlorantha* the six parts of the stigmatic shield are nearly

equally spreading, although close examination reveals that the lobes are paired and alternate with the stamens.

Cheiloclinium meianthum sp. nov.

Frutex scandens ubique glaber, ramulis gracilibus teretibus nodis inconspicue complanato-incrassatis; petiolis rugulosis canaliculatis 10–14 mm. longis, laminis subcoriaceis in sicco viridi-olivaceis subtus pallidioribus, oblongo-ellipticis, 8–11 cm. longis, 3.5–5 cm. latis, basi obtusis et in petio-

Fig. 1. *Tontelea chlorantha:* *a.* flowering branchlet, × ½; *b.* flower, × 7; *c.* flower with sepals and three petals removed, showing disk, stamens, and stylar column, × 7; *d.* petal, inner surface, × 7.

lum decurrentibus, apice breviter (ad 5 mm.) et obtuse cuspidatis, margine integris incrassatis et haud recurvatis, costa utrinque prominente, nervis lateralibus utrinsecus 9–11 patentibus marginem versus leviter arcuatis utrinque inconspicue prominulis, rete venularum immerso; inflorescentiis in axillis foliorum solitariis 4–5.5 cm. longis 5–8-plo dichotome divisis, ramulis brevibus rectis gracilibus, pedunculo 2–2.5 cm. longo, bracteis bracteolisque papyraceis acutis deltoideo-ovatis 0.5–1 mm. longis, ramulis ultimis unifloris, floribus in dichotomiis nullis; pedicellis sub anthesi circiter 1 mm. longis, floribus sub anthesi circiter 2 mm. diametro; sepalis membranaceis semiorbicularibus circiter 0.3 × 0.5 mm. rotundatis erosulis; petalis submembranaceis oblongis, 1–1.3 mm. longis, 0.8–1 mm. latis, apice rotundatis, integris, obscure glandulosis, linea media paullo incrassatis; disci labiis 3 minutis circiter 0.1 mm. altis et 0.3 mm. latis; staminibus 3, filamentis subteretibus circiter 0.4 mm. longis, antheris

circiter 0.2 × 0.3 mm. modo generis dehiscentibus; ovario depresso-subgloboso sub anthesi 0.7–0.8 mm. diametro, stigmatibus 3 obscure deltoideis simplicibus circiter 0.1 mm. longis, ovulis 2 in quoque loculo collaterali-superpositis; fructibus juvenilibus ovoideis, pericarpio duro ruguloso.

BRAZIL: Matto Grosso: Salto Belo, Rio Sacre, just below falls, *J. T. Baldwin, Jr. 3122* (A, TYPE, US), Oct. 23, 1943 (woody vine; fruit about the size of a hen's egg and yellowish [not available with specimen]).

Clearly a member of the species-group *Serrata* as outlined in my recent treatment (in Brittonia 3: 528. 1940), *C. meianthum* is most closely related to *C. Jenmani* A. C. Sm., of British Guiana, from which it differs in its smaller leaf-blades, with the apex more shortly cuspidate, the secondary nerves more numerous and less sharply curved, and both secondaries and veinlets much less obvious, and in its slightly more compact inflorescences. The flowers of the two species are essentially identical, but *C. Jenmani* has flowers borne in the ultimate dichotomies, which does not appear to be the case in the new species.

Loesener, in a recent treatment (in Nat. Pfl. ed. 2. 20b: 171. 1942), has unaccountably referred *Cheiloclinium* to the Celastraceae, although *Kippistia* Miers is placed in the synonymy of *Salacia* (op. cit. 221) as *Salacia* § *Kippistieae*. The congeneracy of *Cheiloclinium* and *Kippistia* seems beyond question, and the remarkably distinct characters of the group set it far apart from *Salacia* (for discussion see Brittonia 3: 526–528. 1940).

VACCINIACEAE

One of the most interesting aspects of the extensive collections made in Pacific Colombia in recent years by Messrs. Killip and Cuatrecasas has been the discovery at low elevations of numerous representatives of the Vacciniaceae. This family, in tropical America, is predominantly montane — to such an extent that only a few years ago representatives from an elevation of less than 1000 m. were rarities. Supposed exceptions were *Anthopterus Wardii* Ball and *Macleania pentaptera* Hoer., which already at the time of my study of the group in 1932 (Contr. U. S. Nat. Herb. 28: 311 seq.) had been collected in mangrove swamps around Buenaventura. It now appears that six members of the Vacciniaceae occur in mangrove swamps in this general area, although, to my knowledge, species of the family are nowhere else in America reported from this habitat. Several other species of Pacific Colombia are reported from tidal forest or from essentially sea-level forest.

No fewer than 42 species of Vacciniaceae are now known from Pacific Colombia at elevations of 1000 m. or less. In view of the fact that only a few of these were known and included in my treatment of 1932, that work is entirely inadequate as far as the family in western Colombia is concerned. Therefore it has seemed advisable to list all those species known from the Pacific slopes of Colombia at altitudes of 1000 m. or less. In the following list, the species are those of the present writer unless another authority is indicated; entities described as new in the present treatment are marked by an asterisk.

Anthopterus bracteatus (although the original collection bears the inscription "Timbiquí above Popayán," it is likely that the town close to the Pacific coast near sea-level is intended).

Anthopterus cuneatus (reported from Nariño at 1000 m. alt.).

Anthopterus Wardii Ball (sea-level, sometimes in mangrove swamps, and upward to 1200 m.).

Calopteryx insignis* (near sea-level).

Cavendishia adenophora Mansf. (from about 700 m. upward to 2000 m. alt. or more).

Cavendishia chlamydantha (near sea-level).

Cavendishia chocoensis (at low elevations, El Chocó).

Cavendishia coccinea (350–450 m. alt., and also reported at 2500 m.).

Cavendishia compacta (near sea-level, and also reported at 1800 m.).

Cavendishia hispida (at low elevations, El Chocó).

Cavendishia micrantha (at low elevations).

Cavendishia palustris (sometimes in mangrove swamps).

Cavendishia praestans (at low elevations, and sometimes in mangrove swamps).

Cavendishia Quereme (H. B. K.) Benth. & Hook. f. (from about 400 m. upward to about 1700 m. alt.).

Cavendishia splachnoides (at low elevations, El Chocó).

Cavendishia striata (from about 100 m. upward to about 2000 m. alt.).

Cavendishia tenella (alt. 200–350 m.).

Cavendishia urophylla (sea-level to 100 m. alt.).

Cavendishia venosa (near sea-level, and also upward to 1000 m. alt. or more).

Cavendishia violacea (near sea-level).

Killipiella styphelioides (at low elevations, El Chocó).

Macleania pentaptera Hoer. (sea-level, often in mangrove swamps, and upward to 1000 m. alt. or more).

Macleania tropica (near sea-level).

Psammisia aberrans (alt. 350–450 m.).

Psammisia caloneura (Nariño, probably at about 900 m. alt.).

[*Psammisia chionantha* Sleumer (northwestern Ecuador at low elevations, to be expected in adjacent Colombia).]

Psammisia coccinea Sleumer (at low elevations).

Psammisia macrocalyx (alt. 350–450 m.).

Psammisia occidentalis (at low elevations, sometimes in tidal forest or at edges of mangrove swamps).

Psammisia pacifica (near sea-level).

Psammisia pedunculata (at low elevations, El Chocó).

Satyria bracteolosa (near sea-level).

Satyria dolichantha (near sea-level, in tidal forest).

Satyria grandifolia Hoer. (near sea-level and upward to 1400 m. or possibly 2100 m. alt.).

Satyria leptantha (alt. 900–1180 m.).

Sphyrospermum buxifolium Poepp. & Endl. (in tidal forest and upward to 2000 m. alt. or more).

Sphyrospermum ellipticum Sleumer (near sea-level, and upward to 1000 m. alt. or more).

Sphyrospermum majus Griseb. (at low elevations, sometimes in mangrove swamps, and upward to about 2000 m. alt.).

Thibaudia Andrei (Nariño, probably at low elevations).

Thibaudia Archeri (at low elevations).

Thibaudia pachyantha (Nariño, at about 900 m. alt.).

Thibaudia pachypoda (near sea-level).

Thibaudia paniculata (Timbiquí, El Cauca; see note under *Anthopterus bracteatus*).

Sphyrospermum buxifolium Poepp. & Endl. Nov. Gen. & Sp. 1: 4. *pl. 8.* 1835; A. C. Sm. in Brittonia 1: 207. 1933.

COLOMBIA: El Chocó: Banks of Quebrada Togoromá, in dense tidal forest, *Killip*

& *Cuatrecasas 39082* (US) (epiphyte, with drooping branches; corolla white); El Valle: Río Calima (región del Chocó), La Trojita, 5–50 m. alt., *Cuatrecasas 16651* (GH) (frutículo epifito; hoja coriácea, rígida, verde; ramas rojizas; corola blanca; baya lilacina, pálida).

This species has seldom if ever been recorded from lower elevations than 750 m.

Sphyrospermum majus Griseb. Fl. Brit. W. Ind. 143. 1859; A. C. Sm. in Brittonia 1: 209. 1933.

COLOMBIA: El Valle: Buenaventura Bay, in mangrove swamp, *Killip 34963* (NY, US) (epiphytic shrub; corolla white); Estero de Bodegas, south shore of Buenaventura Bay, in mangrove swamp, *Killip & Cuatrecasas 38662* (A, US) (dependent epiphyte with white flowers and fruit); Costa del Pacífico, Río Cajambre: Barco, 5–80 m. alt., *Cuatrecasas 17131* (GH) (frútex epifito con ramas rígidas, colgantes; cáliz verdoso amarillento pálido; corola blanca).

Although *S. majus* has been obtained from fairly low elevations, I have not previously seen specimens from sea-level or from mangrove swamps.

Sphyrospermum ellipticum Sleumer in Rep. Sp. Nov. 41: 121. 1936.

COLOMBIA: El Valle: Dense forest along highway from Buenaventura to Cali, near sea-level, *Killip & Cuatrecasas 39003* (A, US) (epiphyte with drooping branches; corolla white); Cordillera Occidental, vertiente occidental: Hoya del Río Digua, lado izquierdo: Piedra de Moler, bosques, 900-1180 m. alt., *Cuatrecasas 14920A* (GH).

The cited specimens agree perfectly with Sleumer's original description of *S. ellipticum*, previously known only from northwestern Ecuador at low elevation. The species is more likely to be confused with *S. majus* than with *S. buxifolium*, but it is readily recognized by its minute corollas and comparatively large obtuse leaves. Probably *Archer 1872*, from Quibdó, on Río Atrato, El Chocó, which I cited as dubiously representing *S. majus* (in Brittonia 1: 210. 1933), is also referable to *S. ellipticum*.

Macleania tropica sp. nov.

Frutex epiphyticus, ramulis elongatis teretibus gracilibus glabris castaneis mox decorticantibus; foliis glabris vel disperse et minute pilosis, petiolis gracilibus 2–3 mm. longis, laminis in sicco chartaceis viridi-olivaceis oblongo-lanceolatis, (3–) 4–6 cm. longis, 1.3–2 cm. latis, basi obtusis vel cuneatis, superne in acuminem peracutum 5–12 mm. longum gradatim attenuatis, margine leviter recurvatis, costa et nervis utrinsecus 2 paullo supra basim orientibus adscendentibus supra subplanis vel leviter insculptis subtus valde elevatis, rete venularum utrinque haud viso; floribus axillaribus solitariis vel binis, pedicellis, calyce et corolla obscure puberulis glabrescentibus, pedicello gracili sub anthesi 7–10 mm. longo basi bracteis 6–8 circumdato, bracteis parvis imbricatis papyraceis oblongo-deltoideis, interioribus circiter 1.5 mm. longis; calyce sub anthesi 6–8 mm. longo inconspicue angulato, tubo 2–3 mm. longo et lato, limbo papyraceo erecto anguste cylindrico-vasculari 4–5 mm. longo 5-dentato, dentibus minute apiculatis, sinibus complanatis; corolla tenuiter carnosa cylindrico-urceolata, sub anthesi 23–25 mm. longa, basim versus 3.5–4.5 mm. diametro, superne contracta, intus glabra, lobis 5 deltoideis subacutis circiter 2 mm. longis; staminibus 10, 12–14 mm. longis, filamentis in tubum glabrum 6–8 mm. longum connatis, antheris 6–7 mm. longis, tubulo unico quam thecis paullo breviore, rima circiter 1.5 mm. longa; stylo filiformi corollam subaequante truncato.

COLOMBIA: El Valle: Costa del Pacífico, Río Cajambre: Barco, 5–80 m. alt., *Cuatrecasas 17103* (GH, TYPE), 21–30 abril, 1944 (arbusto epifito; hoja coriácea, verde oscuro en el haz, claro en el envés; cáliz verdoso rosado; corola roja).

The new species is closely related only to the montane *M. antioquiae* Fedtsch. & Basil., differing in its more gradually attenuate and sharply pointed leaf-blades, its faintly angled rather than obviously winged calyx, its much longer calyx-limb, its longer corolla, which is strictly glabrous within rather than pilose at the throat, and its longer stamens.

Psammisia pedunculata sp. nov.

Frutex gracilis interdum epiphyticus ubique filamentis exceptis glaber, ramulis elongatis gracilibus teretibus cinereis; petiolis rugulosis subteretibus 1–4 mm. longis; laminis chartaceis vel pergamentaceis in sicco fusco-viridibus lanceolato-oblongis, (6–) 9–13 cm. longis, (2–) 2.5–4.5 cm. latis, basi late obtusis, in apicem gracilem 1–2 cm. longum subacutum conspicue caudato-acuminatis, margine integris, 5 (vel 7-)-nerviis, costa nervisque principalibus adscendentibus ad 1.5 cm. concurrentibus supra impressis subtus prominentibus, nervis extimis marginalibus brevibus utrinque haud prominulis, rete venularum intricato utrinque prominulo; inflorescentia apicem ramulorum versus axillari suberecta racemosa 5–13-flora pedunculo conspicuo 3.5–9.5 cm. longo incluso 6–12 cm. longa, pedunculo (inferne interdum inconspicue bracteolatis) et rhachi subteretibus gracilibus; pedicellis teretibus sub anthesi 11–18 mm. longis et 0.5–1 mm. diametro (superne incrassatis), bracteis submembranaceis deltoideis acutis circiter 1.5 mm. longis cito caducis subtentis, basim versus inconspicue bibracteolatis, infra articulationem conspicuam minute glanduloso-denticulatis; calycis tubo cupuliformi sub anthesi circiter 2 mm. longo et 3.5 mm. diametro basi rotundato, limbo submembranaceo erecto-patente circiter 1.5 mm. longo, lobis 5 late deltoideis apiculatis, sinibus complanatis; corolla in sicco membranacea (in vivo ut videtur carnosa) subgloboso-urceolata, circiter 5 mm. longa et medium inflatum versus 7 mm. diametro, basi et apice valde contracta, faucibus circiter 2 mm. diametro, lobis 5 suberectis deltoideis obtusis circiter 1 $\times$ 1.5 mm.; staminibus 10 circiter 3.5 mm. longis, filamentis liberis membranaceis ligulatis circiter 2 mm. longis superne obscure hispidulo-ciliolatis apicem thecarum versus antheris connectis, connectivo brevi nigrescente inconspicue et obtuse calcarato, antheris 2.5–3 mm. longis crassis (circiter 1 mm. diametro), thecis 1.7–2.3 mm. longis valde granulosis basi incurvis et obtusis, tubulis anguste conicis 0.6–1 mm. longis basi subconnatis, rimis ovalibus tubulos subaequantibus; stylo crasso tereti corolla subaequali, stigmate truncato; fructibus obovoideo-globosis rugulosis 7–8 mm. diametro limbo calycis persistente coronatis.

COLOMBIA: El Chocó: La Concepción, 15 km. east of Quibdó, alt. about 75 m., *W. A. Archer 2002* (NY, US no. 1,519,095, TYPE), April 20–May 23, 1931 (slender shrub 1–3 m. high; pedicels Chinese red; corolla pale green), *Archer 2209* (US); Corcovado region, upper Río San Juan, ridge along Yeracüí Valley, alt. 200–275 m., in dense forest, *Killip 35304* (NY, US) (on tree; branches of inflorescence and calyx red; leaves lustrous above); dense forest south of Río Condoto, between Quebrada Guarapo and Mandinga, alt. 120–180 m., *Killip 35681* (NY, US) (epiphyte).

The specimens cited above were originally referred to *P. breviflora* (Benth.) Kl., a montane Colombian species which probably does not occur below 1500 m. However, *P. breviflora* is the closest ally of the new

species, which differs in having its inflorescence much longer and with a conspicuous peduncle, its pedicels shorter, its corolla usually shorter and proportionately more inflated at the middle, and its stamens smaller and proportionately stouter.

Psammisia occidentalis A. C. Sm. in Am. Jour. Bot. 27: 452. 1940.

COLOMBIA: El Chocó: Banks of Quebrada Togoromá, in dense tidal forest, *Killip & Cuatrecasas 39110* (A, US); El Valle: Río Calima (región del Chocó), La Trojita, *Cuatrecasas 16278* (GH); Punta Arenas, north shore of Buenaventura Bay, *Killip & Cuatrecasas 38640* (A, US) (non-inundable woods at edge of mangrove swamp); Agua Clara, along highway from Buenaventura to Cali, *Killip & Cuatrecasas 38869* (A, US); Río Cajambre, Barco, *Cuatrecasas 17009* (GH); Río Yurumanguí, Veneral, *Cuatrecasas 15801* (GH); El Cauca: Río Micay, orilla derecha, en Caliche, *Cuatrecasas 14188* (GH).

The cited collections indicate that this species is fairly abundant along the Pacific coast of Colombia and extend its known range slightly southward. All were obtained at elevations of less than 100 meters, some being from sea-level. The cited material includes specimens with excellent flowers, which in size are similar to the larger flowers mentioned in my original description; the type of the species has rather smaller flowers, which are apparently not fully mature. The plant is said to be either an epiphytic or terrestrial shrub; the pedicels and calyces are red, and the corolla is yellow or greenish with green lobes.

Psammisia macrocalyx sp. nov.

Frutex magnus ramulosus 5–6 m. altus corolla filamentisque exceptis glaber, ramis subscandentibus, ramulis crassis obtuse angulatis demum subteretibus; petiolis nigrescentibus rugulosis crassis (2.5–3 mm. diametro) circiter 2 cm. longis; laminis in sicco chartaceo-coriaceis fusco-olivaceis oblongo-ellipticis, 20–25 cm. longis, 8.5–10 cm. latis, basi obtusis et in petiolum decurrentibus, apice in acuminem 8–12 mm. longum obtusum abrupte cuspidatis, margine leviter recurvato-incrassatis, e basi 5-nerviis, costa nervisque (duobus proximis suprabasalibus) supra acute impressis subtus prominentibus, rete venularum copioso supra leviter subtus valde prominulo; inflorescentiis axillaribus breviter racemosis 5–8-floris basi bracteis 4–6 imbricatis minutis circumdatis, rhachi 13–20 mm. longa rugulosa subflexuosa 1.5–2 mm. diametro, floribus bracteis papyraceis deltoideis obtusis 2–3 mm. longis subtentis; pedicellis crassis (1.5–2.5 mm. diametro) teretibus rugulosis 2–3 cm. longis cum calyce conspicue articulatis medium versus 2- vel 3-bracteolatis, bracteolis subcoriaceis deltoideis subacutis 1.5–2 mm. longis; calyce magno coriaceo campanulato 15–18 mm. longo, apice 10–15 mm. diametro, tubo cupuliformi sub anthesi 5–6 mm. longo, limbo erecto-patente quam tubo duplo longiore in lobis 5 subaequalibus profunde fisso, lobis deltoideo-oblongis subacutis 5–6 mm. longis basi 5–7 mm. latis, sinibus acutis; disco annulari-pulvinato crasse carnoso; corolla carnosa cylindrico-suburceolata 30–38 mm. longa, basim versus 7–10 mm. diametro, faucibus paullo angustata, extus distaliter pilis dispersis adpressis glandulosis brunneis 0.2–0.4 mm. longis pilosa, profunde 5-lobata, lobis erectis oblongis subacutis 6–8 mm. longis basi 3–5 mm. latis; staminibus 10, 12–13 mm. longis, filamentis liberis papyraceis ligulatis 5–6 mm. longis 2–2.5 mm. latis margine distali pilis pallidis 0.2–0.5 mm. longis dense ciliolatis, connectivis

crassis subcoriaceis conspicue bicalcaratis, calcaribus erecto-patentibus obtusis, antheris rigidis circiter 10 mm. longis, thecis circiter 1.5 mm. crassis basi in appendicem subacutam circiter 0.7 mm. longam productis, tubulis quam thecis duplo brevioribus inferne lateraliter connatis superne liberis per rimas ovales circiter 2 mm. longas dehiscentibus; stylo crasso tereti corollam subaequante apice leviter incrassato.

COLOMBIA: El Valle: Cordillera Occidental, vertiente occidental: Hoya del Río Anchicayá, lado derecho, bosques entre Pavas y Miramar, 350–450 m. alt., *Cuatrecasas 14419* (GH, TYPE), 16 abril 1943 (gran frútex de 5–6 metros, muy ramificado; ramas bejucosas; pedúnculos y cáliz rojo-escarlatas mates; corola carmín, brillante, con el extremo esmeralda, luego rojizo).

Psammisia macrocalyx is a very distinct species, with combinations of characters (e.g., very large flowers and short inflorescences) not found in other described species. Its closest relative is probably *P. chionantha* Sleumer, from northwestern Ecuador, but the new species differs in its longer petioles, slightly larger leaf-blades, much shorter racemes, larger calyx (especially as to the coarse deltoid-oblong lobes), glandular-pilose corolla, and distally ciliolate filaments.

Psammisia coccinea Sleumer in Rep. Sp. Nov. 41: 120. 1936.

COLOMBIA: El Chocó: Río San Juan, cercanías de Palestina, 5–50 m. alt., *Cuatrecasas 16929* (GH) (frútex epifito; hoja coriácea, verde claro; cáliz y corola rojo-cárdenos, ⅓ sup. corola blanco); El Valle: Forest along Río Sabaletas, near km. 29 of highway from Buenaventura to Cali, alt. 25 m., *Killip & Cuatrecasas 38858* (US) (epiphytic shrub with elongate branches; old calyx pinkish red); Río Cajambre, Barco, 5–80 m. alt., *Cuatrecasas 17026* (GH) (arbusto bejucoso; hoja coriácea, rígida, verde amarillento medio; cáliz rosado-cárdeno, ápice más claro; corola rosado-cárdena con dientes blancos).

This species, previously recorded only from the type collection from northwestern Ecuador at 150 m. alt., is almost certainly represented by the above-cited Colombian collections. Minor differences between our specimens and the original description are discernible, such as the often caudate-acuminate leaf-apex (1–3 cm. long), the often longer pedicels (7–15 mm. long in flower, up to 40 mm. long in young fruit), the slightly larger calyx (5–8 mm. long), the sometimes shorter corolla (25–28 mm. long at anthesis), and the distally puberulent rather than strictly glabrous filaments. These points appear to be minor variations; in general the species is well characterized by its large 5-nerved leaf-blades, its membranaceous campanulate minutely toothed calyx-limb, its corolla being remarkably thin and papery in texture when dried, and its short stout anthers.

Psammisia pacifica sp. nov.

Frutex epiphyticus corolla juvenili excepta ubique glaber, ramis dependentibus, ramulis elongatis teretibus; petiolis rugosis teretibus crassis (2–3 mm. diametro) 7–10 mm. longis; laminis in sicco chartaceo-coriaceis fuscis anguste oblongo-ellipticis, 17–22 cm. longis, 5–7 cm. latis, basi gradatim angustatis, apice in acuminem 8–15 mm. longum obtusum terminantibus, margine integris, e basi 5-nerviis, costa nervisque duobus proximis apicem fere attingentibus supra valde impressis subtus prominentibus, nervis basalibus duobus marginalibus inconspicuis utrinque prominulis, rete venularum copioso utrinque plus minusve prominulo;

inflorescentiis ex axillis foliorum plerumque delapsorum ortis racemosis 7–15-floris basi bracteis paucis minutis circumdatis, rhachi 3–5 cm. longa leviter angulata 2–3 mm. diametro, floribus bracteis papyraceis oblongis obtusis 4–5 mm. longis mox caducis subtentis; pedicellis teretibus rugulosis crassis (1.5–2 mm. diametro) sub anthesi 16–22 mm. longis, apicem versus conspicue bibracteolatis, bracteolis subcoriaceis oblongo-deltoideis acutis 2–3.5 mm. longis; calyce coriaceo late campanulato sub anthesi 5–7 mm. longo et apice 7–9 mm. diametro, tubo cupuliformi ruguloso 2–3 mm. longo, limbo subpatente quam tubo paullo longiore, lobis 5 late apiculato-deltoideis circiter 1 mm. longis, sinibus rotundatis vel fere complanatis; corolla subcarnosa cylindrico-urceolata sub anthesi 28–35 mm. longa, basim versus 5–7 mm. diametro, faucibus angustata, juventute distaliter obscure et pallide puberula mox glabrescente, profunde 5-lobata, lobis oblongo-deltoideis subacutis 3–4 mm. longis 2–3 mm. latis demum recurvatis; staminibus 10, 11–12 mm. longis, filamentis in tubum subcarnosum circiter 4 mm. longum connatis demum subliberis, connectivis carnosis gracilibus apice bicalcaratis, calcaribus staminum alternorum subobscuris et conspicuis, conspicuioribus patenti-recurvatis obtusis circiter 0.5 mm. longis, antheris 9–9.5 mm. longis, thecis 1–1.2 mm. crassis basi abrupte incurvatis et obtusis, tubulis quam thecis paullo brevioribus inferne connatis apice liberis per rimas ovales circiter 2 mm. longas dehiscentibus; stylo crasso tereti sub anthesi quam corolla paullo longiore apice truncato.

COLOMBIA: El Valle: Costa del Pacífico, Río Cajambre: Silva, 5–80 m. alt., *Cuatrecasas 17616* (GH, TYPE), 5–15 mayo 1944 (frútex epifito con ramas péndulas; hoja coriácea, verde amarillento oscuro; pedúnculos, cáliz y dos tercios corola cárdenos; extremo de la corola blanco).

Psammisia pacifica is a species of the general affinity of the montane *P. macrophylla* (H. B. K.) Kl., from which it differs in having its leaf-blades distinctly narrowed toward the base with the principal nerves oriented from the extreme base, in having its calyx smaller, with a more spreading limb and less obvious lobes, and in having its filaments, at least in fairly mature flowers, connate. In this last character the new species suggests *P. columbiensis* Hoer., a species with smaller leaves, smaller flowers, and more obvious calyx-lobes. From both the mentioned species, *P. pacifica* differs in having the sinuses of its calyx rounded or flattened rather than obviously acute.

Psammisia aberrans sp. nov.

Arbor parva ad 6 m. alta corollis juvenilibus exceptis glabra, ramulis gracilibus teretibus vel hornotinis obtuse angulatis; petiolis rugulosis teretibus crassis (2–3 mm. diametro) 1–1.5 cm. longis; laminis siccitate chartaceis fuscis oblongo-ellipticis, (14–) 18–20 cm. longis, 6–8 cm. latis, basi acutis vel cuneatis, apice in acuminem 13–20 mm. longum obtusum abrupte angustatis, margine leviter recurvatis, e basi 5-nerviis, costa nervisque duobus proximis suprabasalibus apicem fere attingentibus supra leviter impressis subtus prominentibus, nervis basalibus duobus extremis submarginalibus supra paullo subtus valde prominulis, rete venularum conspicuo utrinque prominulo; inflorescentiis e ramulis infra folia ortis breviter racemosis 7–15-floris basi bracteis minutis deltoideis paucis circumdatis, rhachi 1–2 cm. longa obtuse angulata circiter 2 mm. diametro,

floribus bracteis papyraceis oblongo-deltoideis subacutis 2–3.5 mm. longis caducis subtentis; pedicellis teretibus 1–1.5 mm. diametro sub anthesi 13–25 mm. longis medium versus bibracteolatis, bracteolis bracteis basalibus similibus; calyce subcoriaceo campanulato sub anthesi 7–9 mm. longo et apice diametro, tubo cupuliformi circiter 4 mm. longo, limbo erecto-patente tubum subaequante, in lobis 4 vel 5 irregulariter fisso, lobis ovato-deltoideis 1.5–3.5 mm. longis 3–5 mm. latis apice acutis vel apiculatis margine leviter incrassatis, sinibus acutis; corolla subcarnosa cylindrico-urceolata sub anthesi 28–32 mm. longa, basim versus 7–9 mm. diametro, superne angustata, juventute distaliter minute brunneo-puberula glabrescente, lobis 5 oblongis subacutis circiter 3 $\times$ 2 mm.; staminibus 10, 12–13 mm. longis, filamentis submembranaceis liberis ligulatis 3–4 mm. longis, connectivis gracilibus carnosis apice alternatim leviter incrassatis ecalcaratis; antheris 10–11 mm. longis gracilibus, thecis circiter 1 mm. crassis in basim subacutam incurvatam leviter productis, tubulis quam thecis paullo brevioribus liberis vel subconnatis per rimas ovales circiter 2 mm. longas dehiscentibus; stylo crasso tereti corollam subaequante apice truncato.

COLOMBIA: El Valle: Cordillera Occidental, vertiente occidental: Hoya del Río Anchicayá, lado derecho, bosques entre Pavas y Miramar, 350–450 m. alt., *Cuatrecasas 14392* (GH, TYPE), 16 abril 1943 (arbolito de 6 metros; tallo 10 cm. diámetro; pedúnculos y cáliz rosado-cárdenos; mitad o dos tercios inferiores de la corola rojo-cárdenos, parte superior blanca; fruto verde).

Psammisia aberrans is superficially very suggestive of the preceding new species (*P. pacifica*), but it is distinguished by obvious characters pertaining to its calyx, of which the lobes are large and the sinuses acute, and its anthers, which are unspurred. Furthermore, the new species differs from *P. pacifica* in having the inner pair of secondaries of its leaves concurrent with the costa for 5–10 mm., its rachis much shorter, its pedicels less highly bracteolate, and its filaments free. From *P. macrophylla* (H. B. K.) Kl., perhaps a closer relative, the new species differs in its leaf-base, its less prominent fourth and fifth basal nerves, its shorter rachis and pedicels, and its unspurred anthers.

The advisability of placing in *Psammisia* a species with ecalcarate anthers may well be questioned, and indeed will be questioned by students following Macbride's suggestion (in Univ. Wyom. Publ. 11: 43, 44. 1944) that *Psammisia* and *Macleania* be combined and even submerged in *Thibaudia*. Although the presence of anther-spurs has long been used as the most obvious character separating *Psammisia* from *Macleania*, there are also supplementary characters of habit and foliage which serve to distinguish these two groups in the eyes of most students of the family. Other species of *Psammisia*, namely *P. penduliflora* (Dun.) Kl., *P. Hookeriana* Kl., and *P. Ulbrichiana* Hoer., have frequently obscure anther-spurs; but their relationships, like those of *P. aberrans*, are clearly with species of *Psammisia* with spurred anthers.

As to the advisability of reducing *Psammisia* and *Macleania* to *Thibaudia*, this seems to the writer quite unjustified, since at any rate the three groups would presumably be maintained as strong subgenera or sections, thus accomplishing nothing but further confusion of the generally accepted nomenclature. The shifting of coherent groups of species

from generic to subgeneric rank does not necessarily clarify the com-
plexities of reticulate phylogeny.   Admittedly the problem of small vs.
large genera is often solved by personal taste; in the Vacciniaceae I see
no reason at present to combine the genera of "Thibaudieae" into larger
concepts, merely because some students still maintain *Vaccinium* in an
inclusive unwieldy sense.   As to the traditional division of the family into
Vaccinieae and Thibaudieae, this has been considered unsound by recent
students (e.g., the writer in Jour. Wash. Acad. Sci. 33: 243. 1943); but
this fact in itself does not prejudice the status of generic concepts.

Thibaudia pachypoda sp. nov.

Frutex epiphyticus ubique filamentis interdum exceptis glaber, ramulis
apicem versus 3–6 mm. crassis conspicue angulatis, vetustioribus teretibus
cinereis decorticantibus; petiolis crassis (2–3 mm. diametro) 7–15 mm.
longis rugosis leviter biangulatis; laminis rigide coriaceis siccitate olivaceis
ovato-ellipticis. 8–15 cm. longis, 4–8 cm. latis, in basim cuneatam in
petiolum decurrentem angustatis, apicem versus gradatim attenuatis et in
acuminem callosum brevem ad 10 mm. longum cuspidatis, margine integris
et incrassato-recurvatis, subtus disperse brunneo-glanduloso-punctatis,
pinnatinerviis, costa supra paullo subtus valde prominente, nervis
secundariis utrinsecus plerumque 3 adscendentibus curvatis anastomo-
santibus supra prominulis subtus valde elevatis, rete venularum conspicuo
utrinque plus minusve prominulo; inflorescentiis axillaribus breviter race-
mosis 2–5-floris, rhachi crassa angulata 3–10 mm. longa basim versus
bracteis minutis paucis caducis ornata, bracteis floriferis subcoriaceis
oblongis obtusis circiter 3 mm. longis; pedicellis sub anthesi 3–4 cm.
longis crassis (in sicco basi circiter 1.5 mm. diametro superne ad 3–4 mm.
diametro incrassatis, in vivo ut videtur carnosis subteretibus), cum calyce
conspicue articulatis, 1–4 mm. supra basim bibracteolatis, bracteolis sub-
coriaceis deltoideis subacutis circiter 2 mm. longis; calyce coriaceo cupuli-
formi siccitate ruguloso 8–10 mm. longo apice 7–8 mm. diametro, tubo
4–5 mm. longo basi rotundato, limbo erecto tubum subaequante vel
paullo excedente inconspicue 5-denticulato, dentibus 0.3–0.5 mm. longis,
sinibus complanatis, disco pulvinato centro depresso; corolla carnosa
cylindrica sub anthesi 27–31 mm. longa et basim versus 7–8 mm. diametro,
superne gradatim angustata, lobis 5 oblongo-deltoideis obtusis 2–2.5 mm.
longis et latis; staminibus 10 corollam fere aequantibus, 23–26 mm. longis,
filamentis submembranaceis liberis ligulatis 3–5 mm. longis glabris vel
margine interdum obscure pallide ciliolatis, antheris elongatis 21–24 mm.
longis, thecis circiter 1.5 mm. crassis basi subacutis et leviter incurvatis in
tubulos gradatim transeuntibus, tubulis quam thecis duplo brevioribus
per rimas elongatas dehiscentibus; stylo crasso tereti quam corolla paullo
breviore apice leviter incrassato.

COLOMBIA: El Valle: Río Calima (región del Chocó), La Trojita, 5–50 m. alt.,
Cuatrecasas 16616 (GH, TYPE), 19 febr.–10 mar. 1944 (frútex epifito; hoja gruesa,
coriácea, rígida, verde claro; pedúnculo cárdeno; cáliz rosado; corola rosada o rosado-
blanquecina o blanco-violácea) ; Costa del Pacífico, Río Yurumanguí: Veneral, bosques,
5–50 m. alt., *Cuatrecasas 15824* (GH) (frútex epifito; hoja rígida, coriácea, verde
claro ; pedúnculo rojo con el extremo blanco-verdoso ; cáliz verdoso-blanquecino ; corola
blanco-verdosa).

This striking species is characterized by its coriaceous coarsely veined

leaf-blades, stout pedicels, large thick flowers, and very long stamens. Its only close allies are *T. Andrei* A. C. Sm. (known only from Nariño at presumably low elevations) and *T. rigidiflora* A. C. Sm. (from montane Colombia). From *T. Andrei* the new species is distinguished by its cupuliform rather than distinctly apophysate calyx-tube and its proportionately short calyx-limb, from *T. rigidiflora* by its distally tapering and pointed rather than obtuse leaf-blades, its larger (but similarly shaped and proportioned) calyx, and its longer stamens. From both of its allies, *T. pachypoda* differs in its shorter rachis and longer and stouter pedicels and corollas.

Thibaudia Archeri A. C. Sm. in Contr. U. S. Nat. Herb. **28**: 426. *pl. 12.* 1932.

Colombia: El Valle: Costa del Pacífico, Río Cajambre: Barco, 5–80 m. alt., *Cuatrecasas 17259* (GH) (frútex bejucoso; pedúnculos y ramas de la inflorescencia rosado-cárdenos; frutos blancos; corola blanca); Costa del Pacífico, Río Yurumanguí: El Papayo, bosques, 10–20 m. alt., *Cuatrecasas 15986* (GH) (epífito).

These gratifying collections, the second and third of the species, extend its range southward from the type-locality in El Chocó. Our plants are identical with the type in all respects, except that they have frequently larger leaf-blades (up to 32 × 9 cm.) and slightly shorter filaments (3–4 mm. long in mature flowers).

Thibaudia parvifolia (Benth.) Hoer. in Bot. Jahrb. **42**: 275. 1909; A. C. Sm. in Contr. U. S. Nat. Herb. **28**: 428. 1932.

Colombia: El Cauca: Cordillera Central, Páramo del Puracé al sur del Volcán en el filo de la Cordillera: San Francisco, 3400–3450 m. alt., *Cuatrecasas 14593* (GH) (frútex de 2 m.; corola rojo vivo; cáliz rojizo), *14674A* (GH) (frútex; hoja craso-coriácea, verde claro; corola roja).

To my knowledge this attractive small-flowered *Thibaudia* has not otherwise been collected since Hartweg obtained the type, also in El Cauca at high altitude. Although our specimens are identical with the type in all essential details, the following variation should be noted: leaf-blades somewhat broader, not quite so strongly revolute or sulcate as those of the type; pedicel longer, up to 14 mm. long; calyx-tube glandular-strigillose at base; corolla dispersed-glandular-strigillose without as well as faintly puberulent. No. *14593* bears essentially mature fruits, which are ellipsoid, about 10 × 7 mm., rugulose, surmounted by the persistent conspicuous calyx-limb.

Thibaudia aurantia sp. nov.

Frutex ramulosus, ubique (i.e. ramulis, foliis, bracteis bracteolisque, pedicellis, calycibus corollisque) pilis mollibus cinereo-albis patulis 0.5–1 mm. longis dense indutus; ramulis gracilibus subteretibus demum glabrescentibus; petiolis subteretibus inconspicuis 2–3 mm. longis; laminis coriaceis ovatis, 2–3 cm. longis, 1.5–2.2 cm. latis, basi rotundato-subcordatis, apice acutis et calloso-apiculatis, margine integris et valde incrassatis, utrinque minute rugulosis, supra demum subglabrescentibus, costa supra subplana subtus paullo elevata, nervis secundariis utrinsecus 2 vel 3 e basi vel intimis e costa prope medium orientibus utrinque obscuris vel subtus leviter elevatis, venulis immersis; inflorescentia uniflora axillari bracteis 2 linearibus 4–5 mm. longis caducis subtenta, bracteis sub floribus

ut videtur 2 vel 3 papyraceis oblongo-lanceolatis 3–3.5 mm. longis subacutis intus glabris; pedicellis sub anthesi 2–2.5 cm. longis basim versus bracteolas 2 bracteis similes gerentibus, cum calyce inconspicue articulatis; calyce sub anthesi 7–9 mm. longo, tubo cupuliformi circiter 3.5 mm. longo et diametro basi rotundato, limbo erecto-patente tubum paullo excedente papyraceo intus glabro et multinervio profunde 5-lobato, lobis ovatis acute cuspidatis 3–4 mm. longis circiter 3 mm. latis, sinibus acutis, disco annulari-pulvinato glabro; corolla tenuiter carnosa cylindrica sub anthesi 19–21 mm. longa et circiter 7 mm. diametro, intus praeter apices loborum tomentellos glabra, lobis 5 ovato-deltoideis obtusis circiter 1.5 $\times$ 3 mm.; staminibus 10 circiter 11 mm. longis, filamentis membranaceis in tubum 3–3.5 mm. longum dorso distaliter pallide tomentellum connatis, connectivis gracilibus pilosis superne furcatis, antheris 8–8.5 mm. longis, tubulis quam thecis paullo longioribus per rimas ovales 1.2–1.5 mm. longas dehiscentibus; stylo gracili tereti corollam subaequante, stigmate obscure peltato.

COLOMBIA: El Cauca: Cordillera Central, vertiente oriental cerca del filo: Quebrada del Río San Marcos, entre Jardín y San Rafael, 2700–2900 m. alt., *Cuatrecasas 14762* (GH, TYPE), 25 julio 1943 (frútex ramificado; corola anaranjada, ápice blanquecino).

This well-marked species has no close described relatives in Colombia, belonging to a group of species otherwise known from Peru and Bolivia (spp. 36–40 in my treatment in Contr. U. S. Nat. Herb. 28: 410–439. 1932). It is readily distinguished from all of these and from more recently described entities of this group by its pubescent habit, small ovate callose-apiculate leaf-blades with thickened entire margins, one-flowered inflorescences, and deeply lobed calyx-limb.

Thibaudia mundula sp. nov.

Frutex, ramulis teretibus cinereo-puberulis subglabrescentibus; petiolis semiteretibus rugulosis parce puberulis 3–5 mm. longis; laminis coriaceis ovato-ellipticis, 15–21 mm. longis, 9–12 mm. latis, basi late obtusis, apice calloso-apiculatis, margine subintegris (obscure glanduloso-denticulatis) recurvatis incrassatis, utrinque disperse nigro-punctatis juventute minute puberulis mox glabris, costa supra obscure impressa subtus inconspicue elevata, nervis lateralibus paucis venulisque immersis; inflorescentia axillari 1- vel 2-flora bracteis obscuris lineari-oblongis circiter 2.5 mm. longis subtenta, bracteis floriferis papyraceis ovato-deltoideis acutis 1–2 mm. longis extus parce pilosis; pedicellis calycibus corollisque pilis pallidis 0.2–0.5 mm. longis indutis, pedicellis rugulosis subteretibus sub anthesi 10–13 mm. longis basim versus bracteolas 2 bracteis similes gerentibus, cum calyce articulatis; calyce sub anthesi circiter 6 mm. longo, tubo cupuliformi circiter 3 mm. longo et 2.5 mm. diametro basi rotundato obscure brunneo-glanduloso-strigilloso, limbo erecto-patente tubum subaequante papyraceo intus glabro et 5-nervio, lobis 5 deltoideis subacutis circiter 2 $\times$ 2.5 mm., sinibus obtusis, disco annulari-pulvinato glabro; corolla tenuiter carnosa cylindrica sub anthesi 13–15 mm. longa et circiter 5 mm. diametro, intus praeter apicem parce pilosum glabra, lobis 5 deltoideis obtusis circiter 1 $\times$ 2.5 mm.; staminibus 10 circiter 10 mm. longis, filamentis membranaceis in tubum circiter 5 mm. longum dorso distaliter obscure puberulum connatis, connectivis gracilibus pallide pilosis apice furcatis, antheris circiter 6 mm. longis, tubulis thecas subaequantibus per

rimas circiter 2 mm. longas dehiscentibus; stylo gracili corollam sub-aequante apice paullo incrassato.

COLOMBIA: El Cauca: Cordillera Central en la vertiente occidental del macizo del Huila: Cabeceras del Río Palo, Quebrada del Río López, quebradita del Duende, 3450 m. alt., *Cuatrecasas 19144* (A, TYPE), 6 dic. 1944 (frútex epifito; hoja craso-coriácea, verde claro, brillante en el haz, pálido en el envés; cáliz verdoso; corola vermellón).

Although *T. mundula* is obviously most closely related to the preceding new species (*T. aurantia*), numerous characters readily separate the two plants; the most obvious of these are conveniently expressed in a key:

Leaf-blades 20–30 × 15–22 mm., soft-pilose on both sides, rounded-subcordate at base; pedicels 20–25 mm. long; flowers soft-pilose with hairs 0.5–1 mm. long; calyx-limb with many nerves ascending from base and loosely anastomosing, the sinuses deeply acute; corolla 19–21 mm. long; filament-tube 3–3.5 mm. long, the anthers 8–8.5 mm. long..*T. aurantia*.

Leaf-blades 15–21 × 9–12 mm., essentially glabrous, broadly obtuse at base; pedicels 10–13 mm. long; flowers closely pilose with hairs 0.2–0.5 mm. long; calyx-limb with 5 nerves, these terminating in lobes and with few lateral branches, the sinuses obtuse; corolla 13–15 mm. long; filament-tube about 5 mm. long, the anthers about 6 mm. long..*T. mundula*.

Calopteryx gen. nov.

Calyx cum pedicello conspicue articulatus, tubo profunde ruguloso, limbo suberecto 5-lobato. Corolla e basi ad apices loborum conspicue 5-alata. Stamina 10 aequalis quam corolla paullo breviora, filamentis in tubum connatis antheris dorso apicem thecarum versus conjunctis, connectivo inconspicuo angusto, antheris erectis gracilibus, thecis leviter granulosis basi obtusis, tubulis e basi liberis flexibilibus amplis quam thecis multo longioribus per rimas elongatas introrsas dehiscentibus. Stylus quam corolla paullo brevior. Ovarium 5-loculare, placentis axillaribus e basi gracili incrassatis, ovulis minutis numerosissimis obtectis.

Plantae lignosae, ramulis elongatis, foliis alternatis estipulatis petiolatis, laminis magnis e basi plurinerviis. Inflorescentia e ramulis defoliatis orta paniculata ampla, ramulis floribusque bracteis parvis subpersistentibus subtentis, pedicellis bibracteolatis.

The name of this new genus, represented by the single species described below, is derived from καλος, beautiful, and πτερυξ, wing, referring to the long delicate wings of the corolla.

Calopteryx insignis sp. nov.   FIG. 2.

Frutex epiphyticus inflorescentiis exceptis ubique glaber, ramulis floriferis robustis ad 2 cm. diametro cortice sublevi brunneo obductis, ramulis foliiferis gracilibus (2–3 mm. diametro) teretibus cinereis; petiolis subteretibus rugulosis incrassatis (2.5–4 mm. diametro) 7–10 mm. longis; laminis siccitate subcoriaceis fusco-olivaceis oblongo-lanceolatis, 27–36 cm. longis, 6–9 cm. latis, basi obtusis, in apicem caudatum plus minusve 2 cm. longum (apice ipso non viso) gradatim attenuatis, margine integris et leviter recurvatis, e basi 5(vel inconspicue 7-)-nerviis, costa nervisque principalibus adscendentibus elongatis supra impressis subtus prominentibus, nervis marginalibus brevibus inconspicuis utrinque prominulis, rete venularum laxo utrinque subprominulo; inflorescentia in specimine nostro floribus inclusis circiter 11.5 cm. longa et 15 cm. lata, pedunculo ramulisque crassis rugulosis parce brunneo-puberulis demum glabratis, pedunculo brevi

Fig. 2. *Calopteryx insignis:* *a.* flowering branchlet and a branchlet with two attached leaves, × ½; *b.* pedicel and calyx, × 1; *c.* cross-section of ovary, × 2½; *d.* corolla, × 1; *e.* cross-section of corolla, × 1; *f.* apex of corolla, × 1½; *g.* two adjacent stamens, × 2; *h.* style, × 1.

(circiter 1.5 cm. longo) et rhachi 6–7 cm. longis, ramulis primariis circiter 8 patentibus, ramulis secundariis paucis; bracteis sub ramulis pedicellisque papyraceis concavis lanceolatis, 7–11 mm. longis, basi 2–3 mm. latis, in acuminem gradatim attenuatis, extus puberulis, intus glabris; pedicellis sub anthesi 9–18 mm. longis paullo complanatis validis, basi et apice incrassatis, infra articulationem 2–3.5 mm. diametro, pilis circiter 0.2 mm. longis brunneis dispersis indutis, medium versus conspicue bibracteolatis, bracteolis bracteis similibus 4–7 mm. longis circiter 2 mm. latis; calyce cupuliformi sub anthesi circiter 8 mm. longo et apice diametro, ut pedicellis piloso, tubo carnoso profunde ruguloso-sulcato sed non angulato sub anthesi circiter 5 mm. diametro, disco patelliformi subcarnoso glabro margine crenulato-serrulato, limbo membranaceo tubum subaequante intus glabro e basi inconspicue multinervio, lobis ovato-deltoideis acutis 3–4 × 4–5 mm., sinibus acutis; corolla in sicco membranacea in vivo forsan carnosa, sub anthesi 28–35 mm. longa et alis inclusis 7–10 mm. diametro, ut pedicellis parce pilosa, apice ipso circiter 1.5 mm. diametro, alis membranaceis 2–4 mm. latis basi angustioribus distaliter obscure erosulis, lobis paullo incrassatis deltoideis acutis circiter 1 mm. longis latisque; staminibus ubique glabris 25–27 mm. longis, filamentorum tubo membranaceo pallido 5–6 mm. longo, antheris membranaceis 23–25 mm. longis, thecis 4 -5 mm. longis in tubulos 5–6-plo longiores gradatim transeuntibus; stylo filiformi circiter 0.5 mm. diametro, stigmate leviter incrassato truncato.

COLOMBIA: El Valle: Río Calima (región del Chocó), La Trojita, 5–50 m. alt., *Cuatrecasas 16295* (GH, TYPE), 19 febr.–10 mar. 1944 (arbusto epifito; tallo aspecto caneloso; corola rosada o rojiza, dientes blancos).

In its isomorphic stamens with nearly smooth thecae and flexible tubules with clefts of indeterminate length, the entity described above agrees with *Thibaudia* R. & P. and several related genera. From all of these, however, it differs in characters which seem generic in quality. The long corollas with conspicuous wings extending along the entire length, the extremely elongate anther-tubules, and the copiously branching inflorescence are noteworthy characters. *Thibaudia* itself has cylindric or at most lightly angled corollas, and its anthers have tubules rarely more than twice as long as the thecae. In foliage and general type of inflorescence, *Calopteryx* is suggestive of *Thibaudia Archeri* A. C. Sm. and its immediate relatives, and this may indeed represent the closest approach of the new genus to any described group. However, I do not believe that the concept of *Thibaudia* should be expanded to include a plant with such a conspicuously winged corolla and such extremely elongated anther-tubules. Although *Thibaudia* is already a rather heterogeneous aggregate (as noted by the writer in Bull. Torrey Bot. Club 63: 316. 1936), to include *Calopteryx* in it does not seem warranted. A contrary opinion would doubtless be expressed by students agreeing with Macbride, who (in Univ. Wyom. Publ. 11: 37–46. 1944) proposes to include in *Thibaudia* such genera as *Anthopterus* Hook., *Macleania* Hook., *Psammisia* Kl., *Diogenesia* Sleumer, and *Demosthenesia* A. C. Sm. It will be admitted that the characters of *Calopteryx* can be approximated here and there among the above genera; but for that matter so can the

characters of nearly every other genus of Vacciniaceae. In short, the genera in this family must be based upon combinations of characters, the value of various combinations resting upon personal opinion for the time being — but perhaps eventually upon genetic analysis. The alternative to recognizing small genera (although several have 25–100 species) in the Vacciniaceae seems to be to recognize very few, or perhaps only one. Should the latter course be followed, the resulting maze of subgenera, sections, and subsections would be quite unintelligible to the average student; such a treatment would hardly seem likely to clarify the sequence of species-development (*vide* Macbride, op. cit. 44).

Although perhaps it is most closely allied to *Thibaudia,* the new genus should also be compared with *Anthopterus* Hook. and *Plutarchia* A. C. Sm. From the first of these it differs in having its calyx articulate with the pedicel and unwinged, its anther-tubules much longer in proportion, its inflorescence paniculate, and its flowers much larger. *Plutarchia* is a group of north Andean compact small-leaved plants with unwinged corolla and few-flowered, compact, and axillary or subterminal inflorescence; in its elongate flexible anther-tubules *Plutarchia* suggests *Calopteryx.* In habit these three genera are entirely unlike.

Themistoclesia pterota sp. nov.

Frutex interdum epiphyticus, ramulis cinereis teretibus validis glabris; petiolis inconspicuis ad 1.5 mm. longis, foliis subsessilibus interdum subamplexicaulibus; laminis chartaceo-coriaceis in sicco olivaceis ubique glabris oblongo-ovatis, (4–) 6–9 cm. longis, 2.3–4.3 cm. latis, basi profunde cordatis, apice obtusis vel obtuse cuspidatis (acumine ad 5 mm. longo), margine paullo recurvatis, e basi 7- vel 9(raro 11-)-nerviis, costa et nervis interioribus supra leviter elevatis subtus subprominentibus, nervis secundariis valde arcuatis, exterioribus brevibus inconspicuis, rete venularum utrinque subimmerso haud prominulo; inflorescentia axillari pluriflora racemosa vel saepe in ramulos 2 vel 3 adscendentes divisa, rhachi ramulis pedicellisque gracilibus minute puberulis, bracteis sub ramulis floribusque subpersistentibus elliptico-oblongis 1–2 mm. longis; pedicellis 3 -8 mm. longis saepe pluribracteolatis et calyce parce puberulis etiam obscure nigro-pilosis; calyce late turbinato circiter 5 mm. longo et lato, tubo anguste 5-alato, limbo papyraceo erecto-patente lobis inclusis circiter 1.5 mm. longo apice minute 5-denticulato et puberulo-ciliolato; disco conspicuo annulari-pulvinato glabro circiter 1.5 mm. diametro et 0.5 mm. alto; corolla tenuiter carnosa siccitate submembranacea glabra ad apices loborum anguste 5-alata urceolata, 6–7.5 mm. longa, basim versus 4–5 mm. diametro, faucibus ad 1.5 mm. diametro contracta, alis submembranaceis inferne 0.6–1 mm. latis superne angustioribus in lobis exeuntibus, lobis 5 deltoideis subacutis 0.7–1 mm. longis demum recurvatis; staminibus 10 quam corolla paullo brevioribus, filamentis pallidis membranaceis ligulatis alternatim 2–2.5 mm. et 2.5–3 mm. longis, medium versus laxe pilosis superne angustatis, antheris 4–4.5 mm. longis, tubulis quam thecis duplo longioribus per rimas circiter 1 mm. longas dehiscentibus; stylo 5.5–7 mm. longo truncato; bacca modo generis exsucca manifeste angulata quam calyce sub anthesi haud majore.

COLOMBIA: El Valle: Cordillera Occidental, vertiente occidental: Hoya del Río
Sanquininí, lado izquierdo, La Laguna, bosques, 1250–1400 m. alt., *Cuatrecasas 15422*
(GH) (frútex; epifita), *15501* (GH TYPE), 10–20 dic. 1943 (frútex epifito; hoja ccriá-
cea, verde claro, brillante en el haz, verde blanquecino en el envés; cáliz verde claro;
corola blanca; baya azul, blanda).

Themistoclesia pterota, although the essential characters of its flowers
and fruits are those of *Themistoclesia,* differs from the other described
species of the genus in its winged corollas, while the deeply cordate and
subamplexicaul leaves are scarcely suggestive of the genus. Nevertheless,
Themistoclesia seems indubitably to be the correct place for this remark-
able plant. Its alliance is probably with *T. crassifolia* Sleumer, from
which it differs not only in its corolla, but also in its short petioles, its
smaller leaf-blades which are more deeply cordate at base and merely
obtuse or obtusely cuspidate at apex, its sometimes branched inflorescence,
and its shorter pedicels.

Themistoclesia epiphytica A. C. Sm. in Jour. Arnold Arb. 24: 470. 1944.

COLOMBIA: El Cauca: Cordillera Central: Páramo del Puracé al sur del Volcán
en el filo de la Cordillera: San Francisco, 3400–3450 m. alt., *Cuatrecasas 14674* (GH)
(frútex; hoja craso-coriácea verde claro; corola roja).

The cited collection represents a slight extension of range of this species,
previously known from the highlands of Nariño and Putumayo. Both
earlier collections are indicated as epiphytic, but at this altitude it is not
surprising to find individuals of a species either terrestrial or epiphytic.

Cavendishia striata sp. nov.

Cavendishia complectens sensu A. C. Sm. in Contr. U. S. Nat. Herb. 28: 468. 1932,
non Hemsl. nec A. C. Sm. op. cit. 448.

Frutex (semper?) epiphyticus ubique glaber, ramulis teretibus gracilibus
(apicem versus 1.5–3 mm. diametro) interdum ruguloso-striatis; foliis
subsessilibus saepe valde amplexicaulibus, petiolis validis angulatis ad 5
mm. longis sed plerumque subnullis; laminis coriaceis in sicco viridi-
olivaceis late ovatis vel suborbicularibus, (5–)8–18 cm. longis, (5–)7–16.5
cm. latis, basi profunde cordatis, apice rotundatis, margine leviter recurva-
tis, 7–11-nerviis, nervis principalibus secundariis e basi vel ad 3 cm. supra
basim orientibus arcuato-patentibus cum costa supra leviter elevatis vel
subplanis subtus prominentibus, nervis basalibus extimis inconspicuis
submarginalibus utrinque prominulis, rete venularum intricato utrinque
perspicue prominulo; inflorescentia terminali vel subterminali racemosa
8 -12-flora, basi bracteis parvis paucis imbricatis circumdata, pedunculo
subnullo, rhachi sub anthesi 1.5–2.5 cm. longa obscure angulata 1.5–2 mm.
diametro; bracteis floriferis papyraceis oblongo-ellipticis, 8–12 mm. longis,
5–8 mm. latis, apice rotundatis, margine obscure et saepe decidue glandu-
loso-ciliolatis, utrinque nervis adscendentibus parallelis numerosis conspicue
striatis, interdum extus rugulosis; pedicellis teretibus 1–1.5 mm. diametro
sub anthesi 1.5–8 mm. longis basim versus decidue bibracteolatis, bracteolis
papyraceis oblongis subacutis fimbriolatis 2–4 × 1–2 mm.; calyce cam-
panulato sub anthesi 5.5–7.5 mm. longo et apice 3.5–6 mm. diametro, tubo
cupuliformi 2–2.5 mm. longo basi truncato-rotundatis, limbo papyraceo
vel subcoriaceo suberecto 3.5–5 mm. longo intus venis parallelis validis
striato profunde 5-lobato, lobis oblongis 1.5–3 × 1.5–2.5 mm. apice
rotundatis vel obtusis margine glanduloso-ciliolatis et anguste imbricatis,

sinibus acutis; corolla tenuiter carnosa cylindrico-urceolata, sub anthesi 6–10 mm. longa et medium versus 2.5–4 mm. diametro, apice contracta, lobis 5 oblongo-deltoideis subacutis circiter 1 × 1 mm.; staminibus 10 subaequalibus 5–7 mm. longis, filamentis membranaceis ligulatis alternatim 2–2.5 mm. et 3–3.5 mm. longis interdum distaliter inconspicue hispidulis, antheris alternatim 2.5–5.5 mm. et 2–5 mm. longis, thecis 1–2 mm. longis, tubulis quam thecis longioribus fere ad basim fissis; stylo gracili tereti quam corolla paullo breviore, stigmate truncato.

COLOMBIA: El Chocó: Andagoya, alt. 70–100 m., *Killip 35066* (A, NY, US) (epiphytic shrub in second growth forest; bracts white); El Valle: Cordillera Occidental, vertiente occidental: Hoya del Río Digua, lado derecho, La Elsa, bosques, 1000–1200 m. alt., *Cuatrecasas 15306* (GH, TYPE), 9 nov. 1943 (frútex epifito, ramoso, divaricado; hoja craso-coriácea, verde claro, brillante en el haz, mate envés; brácteas rojo carmín; pedúnculos rosados; cáliz verde blanquecino; corola en los tercios inferior y superior blanca, en la mitad negra); Hoya del Río Sanquininí, lado izquierdo, La Laguna, bosques, 1250–1400 m. alt., *Cuatrecasas 15430* (GH) (frútex epifito; hoja craso-coriácea verde claro, rígida; brácteas rosado-cárneas; cáliz blanco; corola en la ½ inf. gris o negra, ½ sup. blanca); El Cauca: "La Gallera," Micay Valley, alt. 1800–2000 m., *Killip 7909* (NY) (in forest); ad pag. El Tambo, La Costa, alt. 800 m., *von Sneidern 838* (NY) (in silva primaeva). [ECUADOR: Pichincha: Nono, *Sodiro 92/36* (Bot. Mus. Berlin, not now available).]

In 1932 I cited two South American collections as representing *C. complectens* Hemsl., the type of which is Costa Rican, but the accumulation of additional good flowering collections from Colombia in the interim has made a reconsideration of this complex desirable. It now seems that rather obvious characters of the bracts and calyx make it inadvisable to include the Colombian material in *C. complectens*, which is, however, closely allied. The chief differences between the two entities may be summarized as follows:

Flower-subtending bracts striate, the principal veins parallel, ascending, strongly raised on both surfaces; rachis 1.5–2.5 cm. long; calyx-lobes oblong, longer than broad (1.5–3 × 1.5–2.5 mm.), narrowly imbricate, striate within with strong parallel veins; western Colombia and Ecuador...........................*C. striata*.

Flower-subtending bracts smooth on both surfaces, not striate, the venation obscurely reticulate, immersed; rachis 3–10 cm. long; calyx-lobes broadly ovate-suborbicular, broader than long (2.5–4 × 3–4.5 mm.), conspicuously and broadly imbricate, narrowed at base, smooth on both surfaces, the venation reticulate, immersed; Costa Rica and Panama...................................*C. complectens*.

In texture of bracts, *C. striata* is suggestive of two Panamanian species recently described by the writer — *C. gaultherioides* and *C. Allenii* — but characters of foliage and flowers readily separate these two species from both the new entity and *C. complectens*. *Cavendishia striata* has an unusually broad altitudinal range, extending from near sea-level up to 1800–2000 m.

Cavendishia compacta A. C. Sm. in Contr. U. S. Nat. Herb. 28: 468. 1932.

COLOMBIA: El Valle: Río Calima (región del Chocó), La Trojita, 5–50 m. alt., *Cuatrecasas 16316* (GH) (arbusto epifito; hoja coriácea, rígida, verde brillante en el haz, mas claro el envés; brácteas rosado-cárdenas; cáliz y corola blancos o blanco-rosados; fruto azul); El Chocó: Entre Carmen de Atrato y Tutunendo, valle del alto Atrato, 500–600 m. alt., *Garcia-Barriga 11124* (US), *11127* (US) (arbol 3–4 m.; brácteas amarillo-rojas; flores rosadas).

The cited specimens are fundamentally similar to the type of this very distinct species, but they are slightly more robust throughout, having leaf-blades up to 9 cm. broad, corollas up to 24 mm. long, and other inflorescence-parts correspondingly large. As in the case of *Satyria grandifolia*, discussed below, there is reasonable doubt as to the actual locality and altitude of the Triana type-specimen. The label of the type-sheet at Kew reads: "Cordillère du Choco, Prov. de Cauca & Choco, hauteur 1800 metr." It is quite possible that the species has a narrower altitudinal range than indicated by the Triana label.

Cavendishia tenella sp. nov.

Frutex ubique glaber, ramulis crassis (distaliter 4–7 mm. diametro) in vivo ut videtur molliter teneribus in sicco acute angulatis; petiolis foliorum maturorum rugulosis validis 1–2 cm. longis canaliculatis superne conspicue alatis; laminis maturis chartaceo-coriaceis in sicco supra metallico-viridibus subtus pallidioribus brunneo-glanduloso-punctatis, elliptico-oblongis, 8 -13 cm. longis, 4–7 cm. latis, basi obtusis et subito in petiolum late decurrentibus, apice obtuse cuspidatis, margine leviter revolutis, plerumque 7-nerviis, costa et nervis 4 superioribus e basi orientibus (vel intimis ad 1 cm. concurrentibus) adscendentibus supra impressis subtus prominentibus, nervis extimis submarginalibus inconspicuis utrinque prominulis, rete venularum copiose intricato utrinque prominulo; inflorescentia subterminali (vel axillari?) racemosa ad 10 cm. longa basi cicatricibus pluribus bractearum caducarum notata, plus minusve epedunculata, multiflora, rhachi crassa (2.5–4 mm. diametro) leviter angulata basi pedicellorum incrassata; floribus ut videtur 35–50, bracteis floriferis submembranaceis ellipticis, circiter 15 mm. longis, paullo angustioribus, apice rotundatis, margine integris scariosis; pedicellis teretibus 3–7 mm. longis crassis (1–1.5 mm. diametro, apice ad 3 mm. conspicue incrassatis) medium versus bibracteolatis, bracteolis subcarnosis oblongis obtusis circiter 1.5 mm. longis margine copiose glanduliferis; calyce carnoso-coriaceo campanulato sub anthesi 7–8 mm. longo et 5–7 mm. diametro, basi rotundato, tubo brevi 1.5–2.5 mm. longo, disco centro depresso, limbo erecto tubum multo excedente, lobis 5 oblongis 4–4.5 mm. longis circiter 5 mm. latis, apice rotundatis vel leviter emarginatis, margine glanduloso-incrassatis et valde imbricatis; corolla molliter carnosa cylindrico-urceolata 10–11 mm. longa, medium versus 5–6 mm. diametro, apice ad 3 mm. diametro contracta, lobis 5 deltoideis obtusis circiter 1 $\times$ 1.5 mm.; staminibus 10 subaequalibus circiter 9 mm. longis, filamentis membranaceis primo subconnatis mox liberis ligulatis, alternatim circiter 2.5 mm. et 3.5 mm. longis, superne angustatis et obscure pilosulis, antheris alternatim circiter 8.5 mm. et 7.5 mm. longis, thecis circiter 3 mm. longis, tubulis thecas excedentibus, rimis elongatis; stylo tereti corollam subaequante, stigmate obscure peltato.

COLOMBIA: El Valle: Cordillera Occidental, vertiente occidental: Hoya del Río Anchicayá, lado derecho, bajando a La Planta, bosques, 200–350 m. alt., *Cuatrecasas 15210* (GH, TYPE), 27 sept. 1943 (gran frútex; brácteas blancas; cáliz verde claro, luego con bordes rosado-violáceos; corola verdoso-pálida con el extremo más o menos rosado, semi-transparente, cérea, con estrecha coronita rosada, con 5 dientes cortos de borde violáceo; ramas muy tiernas (cogollos) con un penacho de hojas cárdeno vivo, ténues, con un invólucro de estípulas blancas).

This striking plant is to be associated with a small group of species

characterized by imbricate calyx-lobes and very short pedicels, occurring from Costa Rica to Pacific Colombia. The closest ally of *C. tenella* is doubtless *C. compacta* A. C. Sm., from which it differs in having its branchlets apparently softer and hence angled in drying, in having its petioles conspicuously angled by means of the long-decurrent bases of leaf-blades, in its differently shaped leaf-base, much shorter leaf-apex, and more basally oriented secondaries, in its more densely flowered racemes, and in its much shorter corolla and stamens.

Cavendishia praestans sp. nov.

Frutex plerumque epiphyticus ubique corollis filamentisque exceptis glaber, ramis saepe crassis nodosis, ramulis subteretibus cinereis rugulosis; petiolis subteretibus rugulosis validis (5–) 8–17 mm. longis; laminis subcoriaceis in sicco fusco-olivaceis oblongis vel anguste elliptico-oblongis, (7–) 15–25 cm. longis, (2–) 5–11 cm. latis, basi truncato-rotundatis vel leviter subcordatis, in apicem plerumque 1–3 cm. longum obtusum vel sub-acutum subito angustatis, margine anguste recurvatis, subtus interdum brunneo-punctatis, 5- vel 7-nerviis, costa et nervis 4 principalibus e basi orientibus vel paullo suprabasalibus supra impressis subtus prominentibus, nervis extimis marginalibus inconspicuis, rete venularum intricato utrinque prominulo; inflorescentia terminali vel apicem ramulorum versus axillari racemosa multiflora basi bracteis numerosis imbricatis (extimis minoribus, intimis bracteis floriferis similibus) circumdata, rhachi robusta 2–4 mm. diametro obtuse angulata (5–) 8–15 cm. longa, bracteis floriferis (juventute valde imbricatis) submembranaceis vel papyraceis ovato- vel obovato-oblongis 15–30 × 10–20 mm. apice rotundatis; pedicellis subteretibus crassis (basi circiter 1 mm. diametro superne ad 2 mm. infra articulationem incrassatis) sub anthesi 5–15 mm. longis, basim versus bibracteolatis, bracteolis papyraceis ovato-oblongis acutis 3–4.5 mm. longis 1.5–2 mm. latis distaliter calloso-incrassatis; calyce oblongo sub anthesi 6–8 mm. longo et apice 5–7 mm. diametro, tubo sulcato 2–3 mm. longo superne leviter constricto, limbo erecto subcoriaceo 4–5.5 mm. longo, lobis 5 deltoideis acutis 1.5–2.5 × 2.5–3 mm. ubique conspicue calloso-incrassatis, sinibus obtusis; corolla in sicco submembranacea (in vivo forsan tenuiter carnosa) cylindrica, 17–23 mm. longa, 5–7 mm. diametro, utrinque leviter angustata, extus pilis 0.5–1 mm. longis pallidis copiose hispidula, lobis 5 oblongo-deltoideis obtusis 1.2–2 mm. longis latisque; staminibus subaequalibus corollam fere aequantibus (15-21 mm. longis), filamentis submembranaceis ligulatis angustis interdum sparse hispidulis alternatim 2.5–5 mm. et 7–10 mm. longis, antheris alternatim 14–19 mm. et 10–13 mm. longis, thecis 6–9 mm. longis basi obtusis, tubulis thecas subaequantibus, rimis elongatis; stylo corollam subaequante tereti circiter 0.5 mm. diametro, stigmate truncato; fructibus juvenilibus ad 7 mm. diametro basi incrassatis apice limbo calycis coronatis.

COLOMBIA: El Chocó : Dense forest south of Río Condoto, between Quebrada Guarapo and Mandinga, alt. 120–180 m., *Killip 35127* (A, US) (epiphyte; bracts pink); banks of Quebrada Togoromá, in dense tidal forest, *Killip & Cuatrecasas 39145* (A, US) (epiphytic shrub; calyx pinkish white, shiny; corolla pink, with white hairs); Río San Juan, cercanías de Palestina, 5–50 m. alt., *Cuatrecasas 16917* (GH) (frútex epifito; hoja coriácea, rígida, verde claro; pedúnculos blancos; cáliz blanco-rosado; brácteas rosadas); El Valle : Estero de Bodegas, south shore of Buenaventura Bay, in man-

grove swamp along Río Potedó, *Killip & Cuatrecasas 38678* (A, TYPE, US), June 2, 1944
(shrub; bracts pink; corolla white); Agua Clara, along highway from Buenaventura to
Cali, alt. about 100 m., in dense forest, *Killip & Cuatrecasas 38880* (A, US) (epiphytic
shrub; bracts pink; calyx pinkish white; corolla white); Río Dagua, in forest about 20
km. east of Buenaventura, alt. about 40 m., *Killip & Garcia 33305* (US) (shrub, along
stream; bracts red; corolla white); Costa del Pacífico, Río Cajambre: Quebrada del
Corosal, 0–5 m. alt., *Cuatrecasas 17733* (arbusto epifito; hoja coriácea, rígida, verde
brillante haz, claro y brillante envés; brácteas rosado-cárdenas; corola peluda, blanca);
Estèro del Cangrejal, entre las bocanas de los Ríos Yurumanguí y Naya, *Cuatrecasas
16020* (GH) (arbusto epifito del mangle; brácteas y cáliz rosados; corola blanca; hoja
rígida coriácea, verde pálido); Antioquía: Guapá, 53 km. south of Turbo (Golfo
de Uraba), alt. about 60 m., *Haught 4603* (A, US) (epiphytic shrub in crown of
forest; bracts pink; corolla white).

From *C. hispida* A. C. Sm., its closest ally, the new species differs
primarily in having its branchlets and leaves, even in a young state,
strictly glabrous rather than copiously hispid-pilose. The leaf-blades of
C. hispida are more or less subbullate, the principal veinlets being im-
pressed above, whereas in *C. praestans* the veinlets are prominulous on
both surfaces. The inflorescence of the new species is more robust and
more copiously floriferous than that of *C. hispida,* and its corollas (simi-
larly pubescent) are somewhat shorter. Although these differences are
not of a striking nature, they are constant among the available specimens.
Admittedly the group composed of these two species, *C. bomareoides,* and
C. splachnoides needs further consideration on the basis of more ample
material.

The occurrence of the new species in the Atlantic littoral of Antioquía is
particularly interesting, suggesting that other species of the Pacific coast
are to be expected around the mouth of the Río Atrato.

Cavendishia violacea sp. nov.

Frutex epiphyticus post anthesin ubique glaber, ramulis apicem versus
gracilibus (2–3 mm. diametro) dense foliatis leviter angulatis subviolaceis
mox subteretibus et cinereis; petiolis 2–5 mm. longis subteretibus rugulosis;
laminis coriaceis subbullatis oblongis, (4–) 7–10 cm. longis, (1.7–) 2.5–
4.5 cm. latis, basi truncato-rotundatis, apice in acuminem 1–2 cm. longum
acutum attenuatis, margine paullo recurvatis, pinnatinerviis, costa supra
conspicue elevata subtus prominente, nervis secundariis utrinsecus 3–5
e costa infra medium orientibus adscendentibus parallelis subrectis supra
in sulculis leviter prominulis subtus valde elevatis, rete venularum copiose
intricato utrinque paullo prominulo; inflorescentia axillari vel terminali
racemosa 10-15-flora basi bracteis imbricatis ad 15 mm. longis (extimis
multo minoribus) circumdata, bracteis floriferis submembranaceis elliptico-
oblongis, 15–17 mm. longis, 7–12 mm. latis, basi et apice rotundatis, incon-
spicue nervatis, pedunculo subnullo, rhachi post anthesin crassa obtuse
angulata 5–10 cm. longa; pedicellis teretibus post anthesin 7–13 mm. longis,
basim versus circiter 1 mm. diametro, apice leviter incrassatis et articula-
tione glandulas parvas oblongas 6–8 gerentibus, basim versus minute
bibracteolatis, bracteolis subcoriaceis oblongis obtusis 0.5–0.7 mm. longis;
calyce post anthesin circiter 5 mm. longo et apice 6 mm. diametro, tubo
brevi valde apophysato basi truncato, limbo erecto quam tubo paullo
longiore carnoso, lobis 5 deltoideis obtusis circiter 1 mm. longis conspicue

calloso-incrassatis, basi discretis, sinibus subcomplanatis; corolla juvenili glabra, staminibus non visis; stylo post anthesin filiformi 12–14 mm. longo, stigmate subpeltato; fructibus irregularibus apophysatis ad 7 mm. diametro, lobis calycis persistentibus inflexis, seminibus oblongo-obovoideis 0.6–0.8 mm. longis conspicue reticulatis.

COLOMBIA: El Valle: Costa del Pacífico, Río Cajambre: Barco, 5–80 m. alt., *Cuatrecasas 17063* (GH, TYPE), 21–30 abril 1944; Río Yurumanguí: Entre Isla de Golondro y La Amargura, 10–40 m. alt., *Cuatrecasas 16048* (GH) (frútex epífito; pedúnculo y brácteas violáceos; cáliz blanquecino liláceo; corola pálido-violácea, cérea; hoja rígida, coriácea, verde claro).

This new species is a relative of *C. amalfiensis* Mansf. and *C. Purdiei* A. C. Sm., differing from both in its more distinctly apophysate calyxtube and the proportionately larger callose-thickened portion of its calyxlobes. From *C. amalfiensis* it also differs in its shorter and proportionately broader leaf-blades, with the upper secondaries more definitely parallel and ascending, in the presence of apical pedicellary glands, and in its shorter corolla (judging from the length of the style in our material). From *C. Purdiei* the new species differs obviously in its larger leaf-blades with a very different type of venation, in its longer inflorescence with more numerous flowers, and in its longer pedicels.

Cavendishia adenophora Mansf. in Notizbl. Bot. Gart. Berlin 9: 439. 1925; A. C. Sm. in Contr. U. S. Nat. Herb. 28: 473. 1932.

COLOMBIA: El Valle: Río Digua Valley, in dense forest along Río Engaña, alt. about 675 m., *Killip 34759* (A, NY, US) (native name: *quereмé*); Cordillera Occidental, vertiente occidental: Hoya del Río Digua, lado izquierdo, Piedra de Moler, bosques, 900–1180 m. alt., *Cuatrecasas 15096* (GH); Hoya del Río Sanquininí, lado izquierdo, La Laguna, bosques, 1250–1400 m. alt., *Cuatrecasas 15394* (GH).

The cited specimens are listed because in 1932 I mentioned 1500 m. as the lowest altitude for the species, which is conspicuous for its brilliant red glandular-margined floriferous bracts. These recently collected specimens from lower elevations are slightly more robust throughout than my earlier description indicates; the leaf-blades are up to 17 × 8.5 cm., the rachis up to 3 cm. long, the basal and floriferous bracts as much as 7 cm. long (the glands of the latter sometimes with stalks 1.5 mm. long), the pedicels up to 17 mm. long (and both glandular and puberulent rather than glabrous as previously stated), the calyx-lobes up to 3 mm. long, and the corollas sometimes 25 mm. long. In spite of these differences from material known from higher elevations in Antioquía and Caldas, I believe that the specimens from El Valle represent merely a more vigorous phase of the species.

It should be noted that these are probably the first collections from El Valle to be accurately referred to *C. adenophora*. In 1932 I placed here two collections from La Cumbre, which Sleumer (in Notizbl. Bot. Gart. Berlin 12: 120. 1934) later — and I think correctly — placed with his *C. nitens*, a species with a caudate-acuminate leaf-apex.

Cavendishia coccinea A. C. Sm. in Bull. Torrey Bot. Club 60: 115. 1933.

COLOMBIA: El Valle: Cordillera Occidental, vertiente occidental: Hoya del Río Anchicayá, lado derecho, bosques entre Pavas y Miramar, 350–450 m. alt., *Cuatrecasas*

14405 (GH) (frútex epifito; ramas finas, resistentes, tortuosas; hoja coriácea verde pálido; brácteas foliáceas carmín con dientes puntiformes verdes, resinoso-viscosas; cáliz rosado-cárdeno con dientes verdosos; corola blanco-lilácea, pálida, viscosa).

This beautiful small-leaved species has previously been known only from the type-collection (*Triana 2698*, "Acostadero, Cordillera del Chocó, alt. 2500 m.") and possibly from a sterile specimen (*Jervise*) from Antioquía. Its occurrence at low elevation in El Valle suggests the possibility that Triana's altitudinal record was inaccurate.

FIG. 3. *Cavendishia urophylla:*   *a.* flowering branchlet, × ½; *b.* flower, × 1; *c.* flower-subtending bract, × 1; *d.* stamens, × 2; *e.* style, × 1; *f.* an inflorescence soon after anthesis, × ½; *figs. a–e* drawn from the type, *fig. f* from *Cuatrecasas 16164.*

Cavendishia urophylla sp. nov.   FIG. 3.

Frutex epiphyticus ubique glaber, ramulis gracilibus subteretibus cinereis; petiolis rugulosis subteretibus vel canaliculatis 4–6 mm. longis; laminis coriaceis in sicco fusco-olivaceis elliptico-ovatis, (4–) 5–8 cm. longis, 1.7–2.7 cm. latis, basi obtusis, in apicem pergracilem acutum 15–30 mm. longum conspicue et abrupte caudato-acuminatis, margine leviter recurvatis, utrinque subnitidis, subtus inconspicue punctatis, e basi 5-nerviis, costa supra leviter impressa subtus elevata, nervis intimis costa similibus inconspicuioribus, nervis extimis immersis haud visis, venulis immersis; inflorescentia terminali vel axillari breviter racemosa ut videtur 2–4-flora bracteis pluribus imbricatis membranaceis involuta, bracteis elliptico-obovatis apice rotundatis integris eglandulosis, maximis (intimis) ad 4 cm. longis et 2–3 cm. latis, rhachi crassa (3–4 mm. diametro) irregu-

lari 3–6 mm. longa inferne cicatricosa; bracteis floriferis submembranaceis vel papyraceis elliptico- vel obovato-oblongis, 8–15 mm. longis, 3–5 mm. latis, obtusis, obscure nervatis, glandulis sessilibus vel breviter stipitatis transverse ellipsoideis copiose marginatis; pedicellis subteretibus sub anthesi 5–7 mm. longis crassis infra articulationem ad 2.5–3 mm. incrassatis, basim versus decidue bibracteolatis, bracteolis bracteis floriferis similibus sed lanceolatis circiter 6–7 × 1 mm.; calyce oblongo-campanulato sub anthesi 8–12 mm. longo et apice 7–8 mm. diametro, tubo leviter ruguloso basi truncato-rotundato, limbo suberecto quam tubo multo longiore, lobis 5 deltoideo-oblongis 2–3 mm. longis latisque subacutis, glandulis subapicalibus elongatis sessilibus etiam glandulis basalibus subglobosis conspicue marginatis, sinibus rotundatis; corolla in sicco submembranacea cylindrica sub anthesi circiter 30 mm. longa et 7 mm. diametro, lobis 5 oblongo-deltoideis subacutis circiter 2.5 mm. longis latisque; staminibus subaequalibus corollam fere aequantibus liberis, filamentis membranaceis ligulatis alternatim 2–3 mm. et 9–11 mm. longis, antheris alternatim circiter 27 mm. et 21 mm. longis submembranaceis, thecis alternatim circiter 16 mm. et 11 mm. longis, tubulis quam thecis paullo brevioribus per rimas elongatas dehiscentibus; stylo gracili tereti corollam fere aequante, stigmate truncato.

COLOMBIA: El Valle: Agua Clara, along highway from Buenaventura to Cali, alt. about 100 m., in dense forest, *Killip & Cuatrecasas 38893* (A, TYPE, US), June 6, 1944 (epiphytic shrub; bracts light pink; calyx white; corolla white at base, bluish-tinged above); Costa del Pacífico: Estero del Encanto, entre los Ríos Yurumanguí y Cajambre, 0–5 m. alt., *Cuatrecasas 16164* (GH) (arbusto epífito; hoja craso-coriácea, verde brillante en el haz, clara en el envés; pedúnculo rojizo en la base; corola blanca verdoso; corola blanca, con el margen de los dientes pardusco); Río Yurumanguí, Veneral, bosques, 5–50 m. alt., *Cuatrecasas 15844* (GH) (frútex epífito; hoja coriácea, verde claro); Río Naya, Puerto Merizalde, bosques, 5–20 m. alt., *Cuatrecasas 14047* (GH) (frútex epífito; hoja y ramas verde tierno).

From its only close ally, *C. coccinea* A. C. Sm., which it resembles in its small caudate-acuminate leaves, the new species differs in obvious inflorescence characters. Its rachis is very short (scarcely 5 mm. long) and few-flowered rather than 4–9 cm. long and many-flowered, its outer sterile bracts are large and conspicuous, its flower-subtending bracts are much smaller and differently shaped, and its anther-tubules are proportionately shorter.

Cavendishia venosa A. C. Sm. in Contr. U. S. Nat. Herb. 28: 474. 1932.

COLOMBIA: El Valle: Costa del Pacífico, Río Cajambre: Barco, 5–80 m. alt., *Cuatrecasas 17042* (GH) (frútex grande epífito; hoja coriácea, rígida, verde claro; brácteas inf. rosado-cárdenas, sup. blancas; cáliz blanco; corola blanca, extremo esmeralda).

Another collection of this distinct and beautiful species is very welcome, particularly as it is accompanied by better data than any of the four collections upon which I based the species. Of these, three were collected by André, including the type, which was without notes. The two remaining André collections came from Altaquer and Armada, both in the valley of the Río Cuaiquer in southern Nariño at altitudes of about 1000 meters (see André, L'Amerique Equinoxiale, pp. 364–366, map on p. 354. 1883). In 1932 I erroneously listed Armada as in Ecuador. The
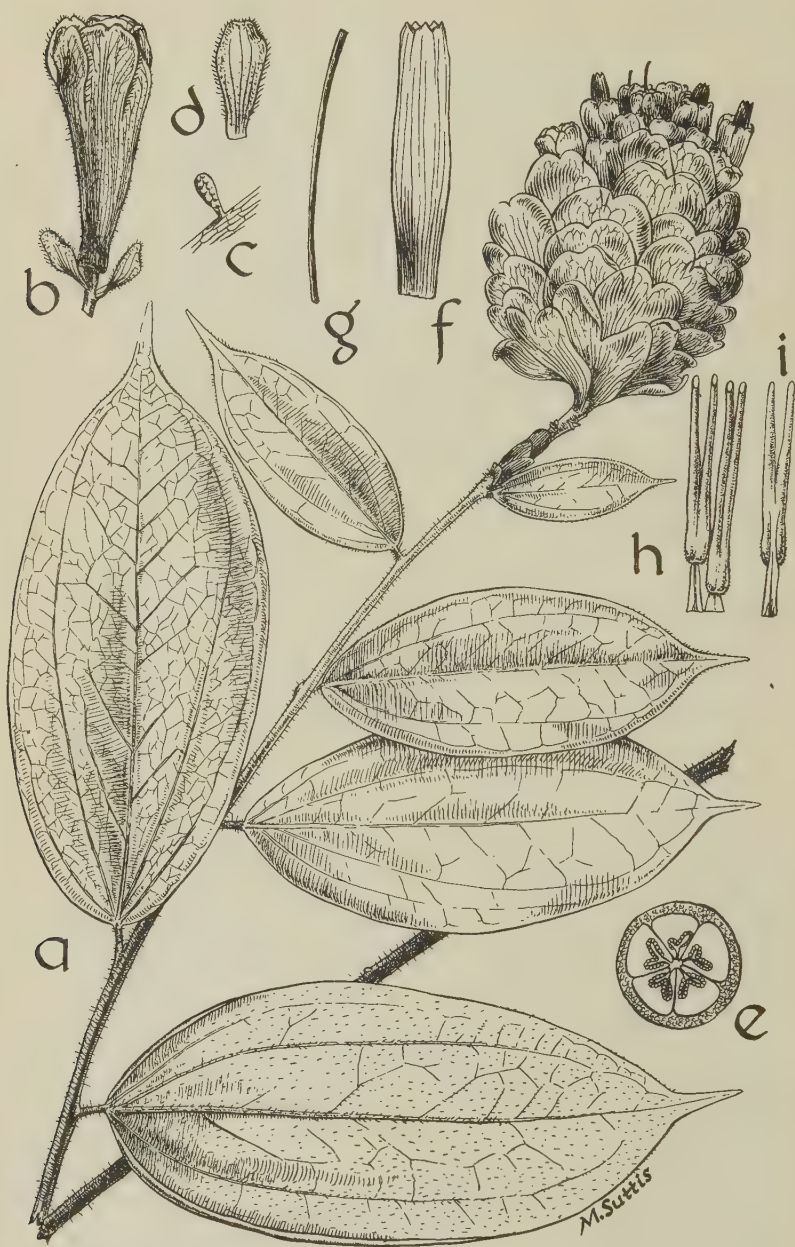
Fig. 4. *Cavendishia chlamydantha*: *a.* flowering branchlet, × ½; *b.* pedicel and calyx, × 1; *c.* gland from calyx-limb, × 50; *d.* pedicellary bracteole, × 2; *e.* cross-section of ovary, × 4; *f.* corolla, × 1; *g.* style, × 1; *h, i.* stamens, introrse and extrorse views, × 2.

Sodiro locality which I cited in 1932, Río Pilatón, is in Pichincha, Ecuador, being one of the headwaters of the Río Esmeraldas.

The Cuatrecasas collection differs from those previously described in having its leaf-blades slightly shorter and broader in proportion, in having its pedicels and calyx-tube softly pale-pilose rather than glabrous (probably younger than those previously seen), and in having its corolla up to 32 mm. long.   I believe that these features are of no more than individual significance.   The stamens (incomplete in earlier collections) are completely glabrous, about 10 mm. long, with slender filaments alternately about 1.5 mm. and 4 mm. long, and with anthers alternately about 9 mm. and 7 mm. long, the tubules being much longer than the thecae.

Cavendishia chlamydantha sp. nov.   FIG. 4.

Frutex epiphyticus, ramulis gracilibus (apicem versus 2.5–4 mm. diametro) subteretibus stramineis pilis ad 2 mm. longis copiose hispidis demum glabrescentibus; petiolis validis (circiter 2 mm. diametro) rugulosis nigrescentibus subteretibus 5–7 mm. longis ut ramulis stramineo-hispidis; laminis in sicco subcoriaceis pallide olivaceis oblongo-ellipticis, 9–17 cm. longis, 3.5–7 cm. latis, basi rotundatis vel late obtusis, in apicem caudatum ad 2 cm. longum subacutum abrupte angustatis, margine integris et anguste recurvatis vel subrevolutis, utrinque pilis inconspicuis circiter 1 mm. longis hispidulis demum subglabratis, 5- vel 7-nerviis, costa supra prominula subtus prominente, nervis 4 principalibus e basi adscendentibus (vel intimis paullo suprabasalibus) curvatis supra prominulis subtus leviter elevatis, nervis extimis submarginalibus inconspicuis, rete venularum laxe intricato utrinque subprominulo; inflorescentia terminali (vel subterminali?) multiflora racemosa ellipsoidea bracteis inclusis ad 12 cm. longa et 8 cm. lata, basi bracteis imbricatis papyraceis oblongis ad 15 mm. longis (extimis minoribus) circumdata, pedunculo subnullo, rhachi crassa (3–4 mm. diametro) ut videtur ad 7 cm. longa basi bractearum incrassata, bracteis inferioribus sterilibus oblongo-obovatis ad 3 $\times$ 2.5 cm. apice rotundatis saepe fissis extus ut calyce glandulosis intus glabris, nervis conspicue anastomosantibus, bracteis superioribus floriferis similibus sed angustioribus ad 4 $\times$ 1.5 cm.; pedicellis subteretibus rugulosis sub anthesi 5–6 mm. longis, infra articulationem ad 2 mm. diametro incrassatis, medium versus bibracteolatis, bracteolis suboppositis membranaceis lanceolato-obovoideis, 8–10 mm. longis, circiter 3 mm. latis, basi angustatis, apice rotundatis vel subemarginatis, paucinerviis, margine obscure ciliolatis, extus ut calyce glandulosis, cito caducis; calyce amplo cum pedicello conspicue articulato, tubo levi oblongo-cupuliformi sub anthesi 3–4 mm. longo et circiter 4 mm. diametro, basi truncato-rotundatis, disco annulari-pulvinato inconspicuo glabro, limbo membranaceo infundibulari corollam fere aequante 28–32 mm. longo, apice circiter 15 mm. diametro, copiose longitudinaliter venoso (nervis superne ramosis non anastomosantibus), extus glandulis stipitatis circiter 0.15 mm. longis copiose obtecto, intus glabro, profunde 5-lobato, lobis obovoideo-oblongis, 12–14 mm. longis et circiter 8 mm. latis, laxe imbricatis, apice emarginatis (et obscure calloso-apiculatis), margine pilis pallidis circiter 1 mm. longis copiose setuloso-ciliatis, sinibus acutis; corolla cylindrica praeter apicem limbo calycis obtecta, in sicco membranacea in vivo ut videtur tenuiter carnosa, sub anthesi circiter 37 mm. longa et

medium versus 7–8 mm. diametro, apice ad 4 mm. diametro angustata, ubique glabra, 5-lobata, lobis oblongo-deltoideis obtusis circiter 1 × 2 mm.; staminibus 10 quam corolla multo brevioribus ubique glabris alternatim circiter 15 mm. et 15.5 mm. longis, filamentis liberis membranaceis stramineis ligulatis alternatim circiter 2 mm. et 5 mm. longis, basi circiter 1.3 mm. latis superne angustatis, antheris alternatim circiter 13.5 mm. et 11.5 mm. longis, thecis leviter granulosis 3–3.5 mm. longis basi rotundatis, tubulis quam thecis subtriplo longioribus apice obtusis per foramines ovales 0.7–1.3 mm. longos dehiscentibus; stylo corollam subaequante tereti circiter 0.6 mm. diametro, stigmate truncato et obscure papilloso.

COLOMBIA: El Valle: Costa del Pacífico, Río Cajambre: Barco, 5–80 m. alt., *Cuatrecasas 17004* (GH, TYPE), 21–30 abril 1944 (frútex epífito; hoja coriácea, verde claro; brácteas inferiores rosadas, las superiores blanco-pálido-verdosas; corola blanca, con el extremo esmeralda; cáliz blanco verdoso).

The entity described above is so unlike the known species of *Cavendishia* in its large membranaceous infundibular calyx-limb, with imbricate lobes enveloping the corolla except at the tip, that it is referred to the genus with hesitation. In the other described species of the genus the calyx-limb, although often exceeding the calyx-tube to a certain extent and occasionally with imbricate lobes, never approaches the corolla in length and is never of such delicate and filmy texture. Furthermore, the stamens of the new species are proportionately very short, less than half as long as the corolla, and the tubules are about three times as long as the thecae and dehisce by short oval introrse pores. As a rule *Cavendishia* has stamens nearly as long as the corolla, with tubules rarely more than twice as long as the thecae and dehiscing by elongate clefts of indeterminate length.

It would seem desirable to base a new genus upon this remarkable species, were it not for the occurrence of certain characters in two other species which demonstrate a transition toward more typical *Cavendishiae*. One of the few species of *Cavendishia* which has comparatively short stamens (only about one-third as long as the corolla) is *C. venosa* A. C. Sm., discussed above as occurring also in the vicinity of Barco. This species also has the tubules unusually long for *Cavendishia*, about three times longer than the thecae; the dehiscence, however, is indeterminate and typically cavendishioid, while the calyx is normal for the genus. Curiously, *C. venosa* is perhaps the species of *Cavendishia* which most nearly suggests the new plant in texture of leaves and inflorescence-bracts; the alliance of *C. chlamydantha* is probably in this vicinity, although it is a remarkably distinct entity.

A second ally of *C. chlamydantha* is *C. micayensis*, described below, a species which provides further transitional features connecting *C. chlamydantha* and the more typical species of the genus.

Cavendishia micayensis sp. nov.

Frutex, ramulis rugulosis subteretibus gracilibus (superne 2–3 mm. diametro) pilis pallidis circiter 1 mm. longis disperse hispidis cito glabrescentibus; petiolis 2–3.5 mm. diametro subteretibus rugulosis nigrescentibus (5–) 8–12 mm. longis ut ramulis hispidis; laminis in sicco chartaceo-

subcoriaceis olivaceis anguste oblongo-ellipticis vel ellipticis, (6–) 12–25 cm. longis, (1.5–) 4–10 cm. latis, basi subacutis vel obtusis, in apicem peracutum ad 1–2.5 cm. longum gradatim caudato-acuminatis, margine anguste revolutis, supra glabris, subtus pilis circiter 1 mm. longis dense hispidulis demum glabratis, 5- vel 7-nerviis, costa nervisque intimis 1–4 cm. concurrentibus supra impressis (basi prominulis) subtus prominentibus, nervis extimis supra subplanis vel prominulis subtus leviter elevatis, rete venularum utrinque prominulo vel subimmerso; inflorescentia subterminali sessili bracteis inclusis 6–9 cm. longa et 3.5–6 cm. lata, basi bracteis imbricatis venosis oblongis ad 15 mm. longis (extimis minoribus) circum-data, rhachi crassa (3–7 mm. diametro) 3.5–7 cm. longa, floribus bracteisque numerosissimis confertis; bracteis inferioribus sterilibus superioribus floriferis papyraceis oblongo-obovatis, 15–27 mm. longis, 9–20 mm. latis, apice rotundatis saepe fissis, margine decidue ciliolatis, conspicue nervosis, extus minute glanduloso-farinosis cito glabratis, intus glabris; floribus in axillis bractearum subsessilibus, pedicellis minutis ebracteolatis; calyce sub anthesi 14–16 mm. longo, tubo oblongo-obconico sub anthesi 3–3.5 mm. longo et summo 2.5–3 mm. diametro, ad basim obtusum gradatim angustato, disco annulari-pulvinato inconspicuo glabro, limbo papyraceo vel submembranaceo infundibulari corollam fere aequante, 11–13.5 mm. (in fructu ad 15 mm.) longo et apice 4–6 mm. diametro, obscure venoso, extus glandulis stipitatis circiter 0.1 mm. longis sparse obtecto, intus glabro, lobis 5 deltoideo-lanceolatis, 3.5–5 mm. longis et 1.5–3 mm. latis, apice subacutis, margine sparse et decidue stipitato-glandulosis, sinibus acutis vel obtusis; corolla tenuiter carnosa subcylindrica, sub anthesi 12–14 mm. longa et basim versus 3.5–4 mm. diametro, faucibus angustata, ubique glabra, lobis 5 oblongo-deltoideis obtusis 1–2 × 1 mm.; staminibus 10 quam corolla paullo brevioribus alternatim 9–11 mm. et 10–12 mm. longis, filamentis liberis membranaceis ligulatis superne angustatis alternatim circiter 1 mm. et 3–4 mm. longis, longioribus margine medium versus pilosis, antheris alternatim 9–10 mm. et 8–9 mm. longis, thecis obscure granulosis 3–4 mm. longis basi obtusis, tubulis quam thecis 1½–2-plo longioribus per foramines ovales 1–1.5 mm. longos dehiscentibus; stylo tereti gracili corollam subaequante, stigmate leviter incrassato et truncato; fructibus rugulosis subgloboso-turbinatis ad 7 mm. diametro (immaturis?) bracteis obtectis calycis limbo persistente coronatis.

COLOMBIA: El Cauca: "La Gallera," Micay Valley, alt. 1400–2100 m., *Killip 7691* (GH, TYPE, Acad. Nat. Sci. Phila., US), June 29 or 30, 1922 (shrub, in forest; bracts red or carmine; corolla white).

Killip 7691 includes two species; the sheet of this number in the herbarium of the New York Botanical Garden is the type of *C. marginata* A. C. Sm. (in Contr. U. S. Nat. Herb. 28: 499. 1932), while the sheets cited above represent an entirely different plant. Although I was aware of this fact in 1932, the flowering specimen at the Gray Herbarium was not then available to me; the National Herbarium and Philadelphia Academy sheets lack the corollas and stamens which make an adequate description feasible.

Cavendishia micayensis is very similar in foliage and general inflores-cence characters to the preceding new species (*C. chlamydantha*), like which it has a calyx-limb of unusual shape and texture which nearly

equals the corolla in length.   The present species differs from *C. chlamy-dantha* in its shorter inflorescence and smaller bracts, its much smaller and essentially sessile flowers with ebracteolate pedicels, its differently shaped calyx-tube, its obscurely veined calyx-limb with comparatively small non-imbricate lobes, its thicker corolla, and its differently proportioned stamens.   In characters pertaining to its calyx, this new species is more or less intermediate between *C. chlamydantha* and typical *Cavendishiae;* in the proportions of its stamens and in their length, *C. micayensis* is quite typical of the genus, but in its anther-dehiscence it is suggestive of *C. chlamydantha*.   In the three species of this general alliance, namely *C. venosa, C. micayensis,* and *C. chlamydantha,* one can observe a remarkable trend within the genus, culminating in *C. chlamydantha*.

Cavendishia palustris A. C. Sm. in Am. Jour. Bot. 27: 543. 1940.

COLOMBIA: El Valle: Río Calima (región del Chocó), La Esperanza, 5–10 m. alt., *Cuatrecasas 16757* (GH) (arbusto bejucoso, epífito; hoja coriácea, verde claro; ramillas inflorescencias y pedúnculos purpúreos; cáliz verde blanquecino; corola blanco-lilácea o blanco-morada); El Forge, near Buenaventura, sea-level, *Killip & Cuatrecasas 38961* (A, US) (epiphytic shrub; corolla white, pink-tinged in upper half; in region inundated only at high tide).

The cited collections agree excellently with the type and only previously known specimen, collected in mangrove swamp in Buenaventura Bay.

Cavendishia micrantha sp. nov.

Frutex epiphyticus staminibus exceptis ubique glaber, ramulis gracilibus subteretibus stramineis vel cinereis; petiolis subteretibus rugulosis 8–17 mm. longis inferne incrassatis; laminis chartaceis in sicco fusco-viridibus oblongo-lanceolatis, (7–) 9–17 cm. longis, (1.3–) 2.5–5.5 cm. latis, ad basim attenuatam in petiolum decurrentem angustatis, apice caudato-acuminatis (acumine gracili acuto 1–2.5 cm. longo), margine integris et paullo recurvatis, 5(vel obscure 7-)-nerviis, costa nervisque 4 supra leviter insculptis vel obscure prominulis subtus plus minusve prominentibus, nervis intimis costa 5–25 mm. concurrentibus apicem fere attingentibus, nervis inferioribus e basi orientibus vel suprabasalibus inconspicuioribus, nervis extimis marginalibus obscuris, rete venularum conspicue intricato utrinque prominulo; inflorescentia axillari vel subterminali racemosa 12–25-flora (floribus saepe mox delapsis) 3 -5 cm. longa, pedunculo subnullo, rhachi simplici obtuse angulata circiter 1 mm. diametro basi ut videtur decidue bracteata, floribus in foveolis insertis, bracteis floriferis papyraceis oblongo-deltoideis subacutis 1–1.5 mm. longis; pedicellis teretibus sub anthesi 12–17 mm. longis, basi circiter 0.7 mm. diametro, superne ad 1–1.5 mm. diametro incrassatis, basim versus obscure 1- vel 2-bracteolatis, bracteolis papyraceis lanceolatis acutis circiter 1 mm. longis obscure glanduloso-marginatis; calyce cupuliformi vel oblongo-pyriformi sub anthesi circiter 4 mm. longo et apice 3–4 mm. diametro, tubo coriaceo basi rotundato, limbo suberecto papyraceo tubum subaequante, lobis 5 deltoideis acutis sub anthesi 1–1.4 mm. longis et ad 1.7 mm. latis, margine sinus acutos versus obscure glanduloso-incrassatis; corolla submembranacea breviter conico-subglobosa, sub anthesi circiter 3 mm. longa et 3.5 mm. diametro, apice ad 1–1.5 mm. diametro contracta, lobis 5 deltoideis acutis circiter 0.6 × 0.8 mm.; staminibus 10 subaequalibus 2–2.4 mm. longis, filamentis

submembranaceis ligulatis 0.6–1.3 mm. longis ciliolato-marginatis, antheris 1.5–2 mm. longis ubique ad apicem pallide hispidulis, tubulis thecas sub-aequantibus, rimis elongatis interdum in thecas extensis; stylo tereti corollam subaequante apice truncato; fructibus juvenilibus rugulosis sub-glaucis globosis ad 5 mm. diametro limbo calycis persistente coronatis.

COLOMBIA: El Valle: Agua Clara, along highway from Buenaventura to Cali, alt. about 100 m., in dense forest, *Killip & Cuatrecasas 38923* (A, US); Costa del Pacífico, Río Cajambre: Barco, 5–80 m. alt., *Cuatrecasas 17000* (GH, TYPE), 21–30 abril 1944 (frútex epífito; hoja coriácea, delgada, verde-grisácea; pedúnculos blanco-verdosos; cáliz blanco verdoso; corola blanca (cerrada); frutos immaturos morado-claros).

This extraordinary species, with the smallest flowers known in *Cavendishia,* scarcely suggests the genus in its floral characters, but in habit it is reminiscent of those atypical *Cavendishiae* related to *C. spicata* A. C. Sm. From *C. chocoensis* A. C. Sm., apparently its closest ally, the new species differs not only in its even smaller flowers, but also in its more obviously hispidulous stamens, longer pedicels, much shorter and essen-tially epedunculate inflorescences, longer petioles, and attenuate-based leaf-blades. A curious relationship between *Cavendishia* and *Psammisia,* not suspected before abundant material from Pacific Colombia became available, is suggested by *C. micrantha* and *C. chocoensis* on the one hand and *Psammisia occidentalis* A. C. Sm. and its relatives on the other.

Cavendishia Quereme (H. B. K.) Benth. & Hook. f. Gen. Pl. 2: 570. 1876; A. C. Sm. in Contr. U. S. Nat. Herb. 28: 495. 1932.

COLOMBIA: El Valle: Cordillera Occidental, vertiente occidental: Hoya del Río Anchicayá, lado derecho, bosque bajando a La Planta, 400 m. alt., *Cuatrecasas 14878* (GH) (frútex epífito; frutos blancos).

The cited specimen is listed because it provides a new low altitude record for this species, which I previously had seen only from elevations of 1000–1700 m.; it is fairly common in El Valle, the type being from the vicinity of Cali.

Satyria dolichantha sp. nov.

Frutex epiphyticus, ramulis apicem versus gracilibus (2–3 mm. diametro) teretibus obscure puberulis, vetustioribus cinereis glabris robustis; petiolis crassis subteretibus rugulosis 6–12 mm. longis juventute puberulis cito glabratis; laminis glabris subcoriaceis in sicco olivaceis oblongo- vel ovato-ellipticis, (8–) 12–17 cm. longis, (3.5–) 4–7 cm. latis, basi late obtusis vel rotundatis, apice in acuminem 5–12 mm. longum obtusum gradatim productis, margine integris et leviter recurvatis, 5(raro 7-)-nerviis, costa supra elevata subtus prominente, nervis 2 intimis cum costa ad 2 cm. con-currentibus vel paullo suprabasalibus adscendentibus apicem versus costa anastomosantibus utrinque elevatis, nervis inferioribus e basi divergentibus submarginalibus inconspicuioribus, rete venularum intricato supra leviter subtus evidenter prominulo; inflorescentia ubique (rhachi, bracteis bracteolisque, pedicellis, calycibus corollisque) minute sed uniformiter pallido-puberula, axillari elongata racemosa 7–12-flora, basi bracteis paucis imbricatis deltoideis obtusis 1–1.5 mm. longis circumdata, pedunculo (circiter 2 cm. longo) et rhachi 4.5–7 cm. longis gracilibus (1–1.5 mm. diametro) leviter angulatis, bracteis floriferis ut bracteis basalibus; pedicel-

lis subteretibus 8–18 mm. longis in vivo ut videtur carnosis, basi 1–1.5 mm. diametro superne ad 2–3 mm. incrassatis, supra basim (1–5 mm.) bracteolas 2 papyraceas ovato-deltoideas acutas 1–1.5 mm. longas obscure ciliolatas gerentibus; calyce sub anthesi 3–5.5 mm. longo, tubo cupuliformi 2.5–3 mm. longo et diametro ruguloso interdum obscure luteo-glanduloso basi rotundato, limbo patente papyraceo intus glabro, lobis 5 ovato-deltoideis apiculatis 0.7–1.5 mm. longis et 2–3 mm. latis, sinibus acutis; corolla in sicco submembranacea in vivo ut videtur carnosa intus glabra cylindrica sub anthesi 40–47 mm. longa, basim versus 4–6 mm. diametro, superne paullo angustata, lobis 5 lanceolato-oblongis obtusis 3–4 mm. longis; staminibus 10 glabris alternatim 10-13 mm. et 11.5–14.5 mm. longis, filamentorum tubo castaneo submembranaceo vel papyraceo 6–7 mm. longo, antheris rigidis alternatim 6.5–8 mm. et 8–9.5 mm. longis, tubulis quam thecis paullo longioribus apice acutis per rimas ovales circiter 2 mm. longas dehiscentibus; stylo tereti sub anthesi leviter protruso apice truncato; fructibus subglobosis rugulosis glabratis 7–9 mm. diametro limbo calycis persistente coronatis.

COLOMBIA: El Chocó: Banks of Quebrada Togoromá, in dense tidal forest, *Killip & Cuatrecasas 39108* (A, TYPE, US), June 13, 1944 (epiphytic shrub; corolla red in lower two-thirds, green in upper third, the tips of the lobes purplish; style greenish white); El Cauca: Costa del Pacífico, Río Micay, Brazo Noanamito, orilla derecha: El Chachajo, 2–5 m. alt., *Cuatrecasas 14249* (GH) (arbusto epifito; cáliz verde; corola carmín con el extremo verde oscuro).

This striking and very distinct species is characterized by its long inflorescences and flowers (the corollas being the longest known for the genus) and its puberulent inflorescence-parts. Its closest relative is *S. panurensis* (Benth.) Benth. & Hook. f., of the Amazon basin and eastern Andean foothills, from which the above-mentioned characters, the more obvious calyx-lobes, and the longer stamens readily distinguish it.

Satyria grandifolia Hoer. in Bot. Jahrb. 42: 319. 1909; A. C. Sm. in Contr. U. S. Nat. Herb. 28: 526. 1932.

COLOMBIA: El Valle: Río Calima (región del Chocó), entre La Esperanza y Bellavista, 5–10 m. alt., *Cuatrecasas 16789* (GH) (gran frútex epifito; hoja coriácea, rígida, verde claro; cáliz rosado cárdeno; pedúnculo rojo cárdeno; corola rojo carmín, ⅓ superior blanco); Cordillera Occidental, vertiente occidental: Hoya del Río Sanquininí, lado izquierdo, La Laguna, bosques, 1250–1400 m. alt., *Cuatrecasas 15592* (GH) (frútex epifito; bayas caulinares blancas, maduras violáceas, 15–20 mm. diám., dulzainas).

Satyria grandifolia has otherwise been recorded only from the type collection of Triana. Although the two specimens cited above have considerable altitudinal range, they are referred here with reasonable confidence, agreeing with the type in foliage and all essential details. No. *15592* has the calyx somewhat more robust than indicated in previous descriptions, the tube being about 4.5 mm. in diameter at anthesis and the limb about 4 mm. long.

The type, *Triana 2694*, was obtained at "Cienegueta," Cordillera del Chocó. Although in 1932 I cited this locality as in El Chocó, it is possible that Triana used this name more broadly and that his locality was actually in El Valle or even El Cauca. The type at Berlin bore the inscription "Prov. del Cauca," and it was so cited by Hoerold. The Berlin sheet also bore the note "Alt. 2100," and Hoerold cited this as 2100 m. If this

is correct, the species would appear to have an unusual altitudinal range of essentially 2100 m., but it is possible that Triana's measurement was inaccurate or that the label was not actually written by him.

Satyria leptantha sp. nov.

Frutex epiphyticus ubique glaber, ramulis crassissimis (floriferis ad 1.5 cm. diametro) teretibus rugosis cinereis; petiolis subteretibus rugosis 1–2 cm. longis crassis (3–5 mm. diametro); laminis coriaceis siccitate olivaceis oblongo-lanceolatis, 23–40 cm. longis, 4–9.5 cm. latis, basi late obtusis et in petiolum leviter decurrentibus, superne angustatis (apice ipso non viso ut videtur acuto), margine integris et leviter recurvatis, 5-nerviis, costa nervisque 2 interioribus adscendentibus cum costa 2.5–6 cm. concurrentibus apicem fere attingentibus supra leviter impressis subtus valde prominenti-bus, nervis 2 inferioribus e basi divergentibus submarginalibus incon-spicuioribus, venulis supra immersis subtus in reticulum laxum prominulum anastomosantibus; inflorescentiis e ramulis defoliatis in glomerulis aggre-gatis fasciculatim breviter racemosis 3–5-floris, bracteis basi rhachis et bracteis floriferis papyraceis deltoideis acutis 1–1.5 mm. longis obscure ciliolatis caducis, rhachi minuta 1–4 mm. longa; pedicellis gracilibus (basi circiter 0.5 mm. diametro, superne ad 2 mm. diametro gradatim incrassatis) teretibus rugulosis 19–24 mm. longis, supra basim (3–7 mm.) bracteolas 2 oblongas obtusas circiter 1.5 mm. longas gerentibus; calyce brevi sub anthesi 2–3 mm. longo, tubo ruguloso circiter 1.5 mm. longo et 3.5 mm. diametro basi truncato, limbo patente 1–1.5 mm. longo papyraceo, lobis 5 ovatis apiculatis circiter 1 × 2.5 mm. praeter partem apicalem incrassato-marginatis, sinibus obtusis; corolla tenuiter carnosa graciliter cylindrica sub anthesi 24–27 mm. longa, basim versus circiter 3 mm. diametro, superne paullo angustata, lobis 5 deltoideis subacutis circiter 0.7 × 1.5 mm.; staminibus 10 alternatim 7 mm. et 8 mm. longis, filamentorum tubo circiter 3 mm. longo, antheris rigidis alternatim circiter 5 mm. et 6 mm. longis, tubulis thecas subaequantibus per rimas apertas ovales circiter 1.5 mm. longas dehiscentibus; stylo gracili tereti sub anthesi corollam excedente apice paullo incrassato.

COLOMBIA: El Valle: Cordillera Occidental, vertiente occidental: Hoya del Río Digua, lado izquierdo, Piedra de Moler, bosques, 900–1180 m. alt., *Cuatrecasas 14963* (GH, TYPE), 19–28 agosto 1943 (frútex grande epifito; pedúnculos rojo-cárdenos; corola rojo-cárdena con el extremo blanco).

Satyria leptantha is closely related only to *S. grandifolia* Hoer., differ-ing in its very long and proportionately narrower leaf-blades with the inner secondaries more highly concurrent, and in its very short and com-paratively few-flowered inflorescences, longer pedicels, very slender corolla, and shorter anthers.

Satyria arborea A. C. Sm. in Jour. Arnold Arb. 24: 469. 1943.

COLOMBIA: Antioquía: Cerro del Tabor, Yarumal, *Daniel 3401* (US) (fr.); Páramo de Sonsón, alt. 2700–2850 m., *Daniel 3438* (US) (fl.).

´ The cited collections are the second and third known of the species, the type of which was obtained between Valdivia and Yarumal, in Antioquía. The fruiting specimen has the petioles often negligible (1–4 mm. long), the leaf-blades (5–) 7–9 cm. long and 2.5–3.5 cm. broad, the pedicels up to 28 mm. long, and the fruits strongly rugulose (apparently very fleshy

when fresh), depressed-subglobose, 5–8 mm. in diameter, flattened at apex, and surmounted by the inconspicuous calyx-limb.

Satyria bracteolosa sp. nov.

Frutex epiphyticus ubique inflorescentia excepta glaber, ramulis apicem versus gracilibus (2–4 mm. diametro) brunneis obtuse angulatis, vetustioribus validis subteretibus cinereis; petiolis 1–2 mm. diametro 5–10 mm. longis rugulosis inconspicue angulatis; laminis coriaceis in sicco olivaceis oblongo-ellipticis, 8–22 cm. longis, 3–7 cm. latis, basi obtusis et in petiolum decurrentibus, apice in acuminem 5–15 mm. longum obtusum vel subacutum cuspidatis, margine integris et leviter recurvatis, 5(vel 7-)-nerviis, costa supra valde elevata subtus prominente, nervis intimis cum costa 1–3.5 cm. concurrentibus, extimis e basi orientibus vel paullo suprabasalibus, nervis omnibus adscendentibus supra prominulis subtus elevatis, rete venularum intricato utrinque subprominulo vel supra immerso; inflorescentiis e ramulis defoliatis ortis glomerulatis vel inconspicue breviter racemosis 4–7-floris basi bracteis pluribus circumdatis, ubique (bracteis bracteolisque, pedicellis, calycibus corollisque) obscure pallido-puberulis, bracteis basalibus imbricatis papyraceis oblongo-deltoideis obtusis 2–3 mm. longis et latis ciliolato-marginatis, rhachi brevissima; pedicellis teretibus crassis (1.5–2 mm. diametro) 5–8 mm. longis apice incrassatis et cum calyce articulatis, apicem versus conspicue bibracteolatis, bracteolis papyraceis late ovatis vel reniformibus, 2–3 mm. longis, 4–5 mm. latis, intus glabris, margine ciliolatis, margine basali imbricatis, apice rotundatis, liberis sed pseudocupulam basim calycis tubi amplectentem formantibus; calyce cupuliformi sub anthesi circiter 4 mm. longo, tubo brevi disco lato pulvinato coronato, limbo papyraceo intus glabro erecto-patente circiter 2 mm. longo, lobis 5 oblongo-deltoideis obtusis circiter 1.5 × 3 mm. interdum subconnatis, sinibus acutis; corolla carnosa intus glabra cylindrico-urceolata, sub anthesi 14–19 mm. longa, basim versus 3–5 mm. diametro, superne gradatim angustata, lobis 5 oblongis subacutis circiter 2–3 × 1.5 mm.; staminibus 10 alternatim 5–6 mm. et 7–8 mm. longis, filamentorum tubo papyraceo glabro 2–2.5 mm. longo, antheris rigidis alternatim 4–4.5 mm. et circiter 6 mm. longis, thecis basi subacutis et leviter productis, tubulis thecas subaequantibus per rimas ovales circiter 2 mm. longas dehiscentibus; stylo tereti apice truncato quam corolla conspicue longiore.

COLOMBIA: El Chocó: Río San Juan, cercanías de Palestina, 5–50 m. alt., *Cuatrecasas 16894* (GH, TYPE), 12–14 mar. 1944 (frútex epifito; hoja coriácea, rígida, verde claro; cáliz id.; corola roja, ⅓ superior amarillo); El Valle: Río Calima (región del Chocó), La Trojita, 5–50 m. alt., *Cuatrecasas 16604* (GH) (frútex epifito; hoja coriácea, rígida, verde medio; cáliz verde claro; corola roja, ¼ superior rojo amarillento, dientes verdosos); Costa del Pacífico, Río Cajambre: Quebrada del Corosal, 0–5 m. alt., *Cuatrecasas 17732* (GH) (arbusto epifito; hoja coriácea, rígida; cáliz verde; corola con el extremo blanco).

This remarkable species differs from all others of the genus in its subapical pedicellary bracteoles, which form a pseudocupule clasping the base of the calyx-tube. Another distinguishing feature is the very short puberulent inflorescence; there is a striking contrast between the long and short anthers, the latter being comparatively inconspicuous and appearing dorsal to the larger ones.

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THE AUSTRALIAN SPECIES OF ANTIRHEA, AND A NEW NAME FOR A CUBAN SPECIES

C. T. WHITE

With one plate

THE GENUS *Antirhea* Commerson ex Jussieu was established in 1789 on the basis of a Mauritius tree, there known as "Bois de Losteau". Since that time many species have been described from widely different places in the tropics and subtropics of both hemispheres, including three from Australia. A search through Index Kewensis and its supplements showed that two of these had not been listed and the third one by error was wrongly entered as to the spelling of the specific epithet. A query from Dr. Lily M. Perry prompted me to look up the Australian species (all of which are confined to Queensland), when the above omissions were noted.

The three species, with correct citations, synonyms, and distribution, are here listed:

Antirhea tenuiflora F. Muell. ex Benth. in Fl. Austr. 3: 418. 1867 (as *Antirrhaea*); F. Muell. Fragm. Phytogr. Austr. 7: 48. 1869 (as *Antirrhoea*); non Urban (1900).
Guettarda tenuiflora F. Muell. Fragm. Phytogr. Austr. 9: 183. 1875, First Census 75. 1882.
Antirrhoea tenuifolia Jackson, Ind. Kew. 1: 155. 1893, sphalm.
QUEENSLAND: From the Johnstone River to Cape York.

By a curious slip this species was listed in the Index Kewensis as *A. tenuifolia,* a mistake repeated in certain other publications. Perhaps this erroneous entry accounts for Urban giving the preëmpted specific epithet *tenuiflora* to a West Indian species. For the latter a name change becomes necessary, and the following is proposed:

Antirhea Urbaniana nom. nov.
Antirrhoea tenuiflora Urban, Symb. Antill. 1: 438. 1900; non F. Mueller (1867).
CUBA.

Antirhea putaminosa (F. Muell.) F. M. Bailey, Queensl. Fl. 3: 760. 1900 (as *Antirrhaea*).
Timonius putaminosus F. Muell. Fragm. Phytogr. Austr. 4: 92. 1864.
Bobea putaminosa F. Muell. loc. cit. in syn. and op. cit. 5: 212. 1866.
Guettardella putaminosa Benth. Fl. Austr. 3: 419. 1867.
Guettarda putaminosa F. Muell. op. cit. 9: 183. 1875.
Antirrhoea putaminosa F. Muell. op. cit. 9: 183. 1875, in syn.
QUEENSLAND: Central coastal region; in "dry rain forest" a few miles north and south of Rockhampton, i. e. the tropic of Capricorn.

Mueller, in the original publication of *Guettarda putaminosa,* credits the binomial *Antirrhoea putaminosa* to "J. Hook. in B[enth]. & H[ook]. Gen. Pl. ii. 100," and F. M. Bailey cites the joint authors also as the

authority. Very few actual combinations were made in the Genera
Plantarum, but none in this instance.   Bentham & Hooker did not men-
tion the species; however, some earlier Australian authors have translated
Bentham & Hooker's inference in many cases as proposed new names.

This species is a small tree common in a rather dry type of mixed forest
characteristic of coastal and mid-inland Queensland and in the more
inland places merging into "Brigalow" (*Acacia*) and "Beelah" (*Casua-
rina*) forest ("scrub").   However, this type of vegetation has been
designated by some as monsoon forest, because some of the larger soft-
wooded trees such as *Gyrocarpus* and *Brachychiton* lose their leaves in
the dry period, although these genera are not always present.   "Box
wood scrub" is a name sometimes given to this forest, for the majority
of the trees are of slow growth and possess a box-like (*Buxus*) wood.
Vegetative parts generally show a tendency toward xerophytism.

Antirhea myrtoides (F. Muell.) F. M. Bailey, Queensl. Fl. 3: 760. 1900 (as
        Antirrhaea).   PL. I.
Guettarda myrtoides F. Muell. Fragm. Phytogr. Austr. 9: 184. 1875.
Bobea myrtoides (F. Muell.) Valeton in Bull. Dep. Agric. Ind. Néerl. 26: 7. 1909.
QUEENSLAND: Rockingham Bay (known only from the type-collection).

Valeton, in his introductory remarks on the genus *Timonius,* said that
Guettarda myrtoides F. Muell. was a true *Bobea* and actually made the
combination in his discussion of the species.   Alston, Hand-book Fl.
Ceyl. 6, Suppl.: 151. 1931, suggested that "though *Nelitris* Gaertn. is one
of the 'nomina rejicienda' of the International Rules, I think that it should
be adopted in preference to *Bobea* Gaud."   By the keys and descriptions
in the Genera Plantarum I judge that this species would come under
Antirhea Comm. ex Juss.   By the key in the Pflanzenfamilien it would
come under *Bobea* Gaud. on account of a rather deeply 2-cleft style.
Unfortunately the plant is known only from the type-collection.   Mr.
Jessep, Government Botanist, National Herbarium, Melbourne, kindly
sent me a part of the type including a single flower, one of three on the
type sheet.   I carefully dissected this as far as I could without destroying
it and found the style to be deeply 2-cleft.

EXPLANATION OF THE PLATE

Part of type specimen of *Antirhea myrtoides* (F. Muell.) F. M. Bailey.

QUEENSLAND HERBARIUM,
    BOTANIC GARDENS,
        BRISBANE, AUSTRALIA.

Ex-National Herbarium of Victoria.

Guettarda myrtoides F.v.M.

Rockingham Bay, N. Q'land.

"Sect. *Antirrhœa*,"
of the genus *Guettarda*
according to F.v.Mueller,
in the type diagnosis.
From nate IX. 194 etc.

TYPE.

leg. J. Dallachy

(*Part of type collection.*)

DATE. 25. 11. 1870.

Antirhea myrtoides (F. Muell.) F. M. Bailey